

6 Population growth

6.1 Introduction

In this chapter we deal with the internal workings of a population that result in a change of population size. The speed of that change is measured as rate of increase. Any such change alerts us that the fecundity rate, the mortality rate, or the age distribution, or more than one of these, has changed. Each of those parameters will be considered in turn and the relationships between them explained.

This chapter has two quite distinct functions. The first is to arm the reader with the theory of population dynamics. The second is to indicate which parts of that theory are immediately applicable to wildlife management and which parts are necessary only for a background understanding. The first function may appear to load a manager with unnecessary mental baggage, but without such knowledge mistakes are more than just possible, they are likely. Knowledge of atomic theory is not needed to mix a medicine, but without that knowledge a pharmacist will, sooner or later, make a critical mistake.

6.2 Rate of increase

If a population comprising 100 animals on (say) January 1 contained 200 animals on the following January 1 then obviously it has doubled over 1 year. What will be its size on the next January 1 if it continues to grow at the same rate? The answer is not 300, as it would be if the growth increment (net number of animals added over the year) remained constant each year, but 400 because it is the growth rate (net number of animals added, divided by numbers present at the beginning of the interval) that remains constant. Thus the growth of a population is analogous to the growth of a sum of money deposited at interest with a bank. In both cases the growth increment each year is determined by the rate of growth and by the amount of money or the number of animals that are there to start with. Both grow according to the rules of compound interest and all calculations must therefore be governed by that branch of arithmetic.

Populations decrease as well as increase. The population of 100 animals on January 1 might have declined to 50 by the following January 1, in which case we say that the population has halved. If its decline continues at the same rate it will be down to 25 on the next January 1. Halving and doubling are the same process operating with equal force, the only difference being that the process is running in opposite directions. The terms by which we measure the magnitude of the process should reflect that equivalence. It is poorly achieved by simply giving the multiplier of the growth, 2 for a doubling and 0.5 for a halving, and it becomes even more confusing when these are given as percentages. We need a metric that gives exactly the same figure for a halving as for a doubling, but with the sign reversed. That would make it obvious that a decrease is simply a negative rate of increase.

It is achieved by expressing the rate of increase, positive or negative, as a geometric rate according to the following equation:

$$N_{t+1} = N_t \lambda = N_t e^r$$

in which N_t is population size at time t , N_{t+1} is the population size a unit of time later, e is the base of natural logs taking the value 2.7182817, and r is the exponential rate of increase. The **finite rate of increase** (λ) is the ratio of the two censuses:

$$\lambda = N_{t+1}/N_t$$

and therefore the **exponential rate of increase** is:

$$r = \log_e(N_{t+1}/N_t) = \log_e \lambda$$

We will try this out on a doubling and halving. With a doubling:

$$\lambda = 200/100 = 2$$

and so:

$$r = \log_e \lambda = 0.693$$

With a halving:

$$\lambda = 50/100 = 0.5$$

and so:

$$r = \log_e \lambda = -0.693$$

Thus a halving and a doubling both provide the same exponential rate of increase, 0.693, which in the case of a halving has the sign reversed (i.e. -0.693). It makes the point again that a rate of decrease is simply a negative rate of increase.

The finite rate of increase (i.e. the growth multiplier λ) and the exponential rate of increase r must each have a unit attached to them. In our example the unit was a year, and so we can say that the population is multiplied by λ per year. The exponential rate r is actually the growth multiplier of \log_e numbers per year. That is something of a mouthful and so we say that the population increased at an exponential rate r on a yearly basis. Note that λ and r are simply different ways of presenting the same rate of change. They do not contain independent information.

Unlike the finite rate of increase, the exponential rate of increase can be changed from one unit of time to another by simple multiplication and division. If $r = -0.693$ on a yearly basis then $r = -0.693/365 = -0.0019$ on a daily basis. That simplicity is not available for λ .

The equations given above were simplified to embrace only one unit of time. They can be generalized to:

$$N_t = N_0 e^{rt}$$

where N_0 is population size at the beginning of the period of interest and N_t is the population size t units of time later. The average exponential rate of increase over the period is:

$$r = [\log_e(N_t/N_0)]/t$$

which can be written also as:

$$r = (\log_e N_t - \log_e N_0)/t$$

It would be a waste of data to use only the population estimates at the beginning and end of the period to estimate the average rate of increase between those two dates. If intermediate estimates are available these can and should be included in the calculation to increase its precision. The appropriate technique is to take natural logarithms of the population estimates and then fit a linear regression to the data points each comprising $\log_e N$ and t . A linear regression takes the form $y = a + bx$ in which y is the dependent variable (in this case logged population size) and x is the independent variable (in this case time measured in units of choice). Our equation thus becomes:

$$\log_e N = a + bt$$

in which a is the fitted value of $\log_e N$ when time $t = 0$ and b is the increase in $\log_e N$ over one interval of time. Note that this is the definition of r , and so $r = b$. The equation for the linear regression may thus be rewritten:

$$\log_e N = a + rt$$

It can be converted back to the notation used in the example where rate of increase was measured between only two points by designating the start of the period as time 0:

$$\log_e N_t = \log_e N_0 + rt$$

which with a little rearranging converts to:

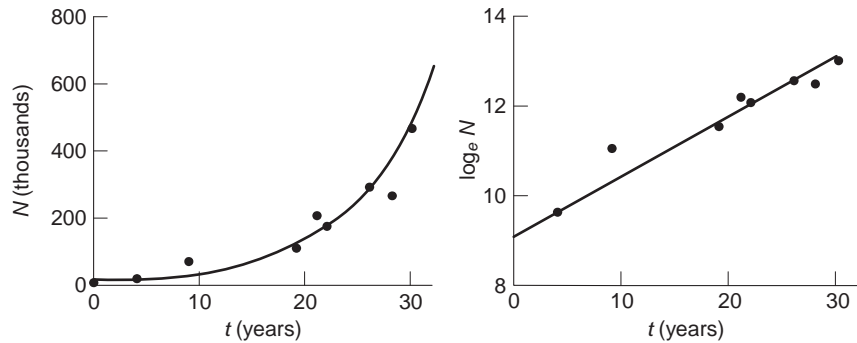
$$r = (\log_e N_t - \log_e N_0)/t$$

as before. Figure 6.1 shows such use of linear regression to estimate the rate of increase of the George River caribou herd in eastern Canada, yielding $r = 0.11$ (Messier *et al.* 1988).

6.2.1 Intrinsic rate of increase

The rate of increase of a population of vertebrates usually fluctuates gently for most of the time, around a mean of zero. If conditions suddenly become more favorable the population increases, the environmental improvement being reflected in a rise of fecundity and a decline in mortality. The environmental change might have been an increase in food supply, perhaps a flush of plant growth occasioned by a mild winter and a wet spring. The rate at which the population increases is

Fig. 6.1 Exponential population growth of the George River caribou herd, as discussed in the text. (After Messier *et al.* 1988.)



then determined by two things: on one hand the amount of food available and on the other the intrinsic ability of the species to convert that extra energy into enhanced fecundity and diminished mortality. Thus, it depends on an environmental effect and an intrinsic effect but neither is without limit. From the viewpoint of the animal both are constrained. There comes a point at which the animal has all the food it can eat, any further food having no additional effect on its reproductive rate and probability of survival. Similarly, an animal's reproductive rate is constrained at the upper limit by its physiology. Litters can be only so big and the interval between successive litters cannot be reduced below the gestation period. The potential rate of increase can never be very high, irrespective of how favorable the environmental conditions are, if the period of gestation is long (e.g. 22 months for the African elephant, *Loxodonta africana*). All species, therefore, have a maximum rate of increase, which is called their **intrinsic rate of increase** (Fisher 1930) and denoted r_m . It is a particularly important parameter in estimating sustainable yield (see Section 19.3).

Populations do not attain that maximum very often. It requires a very high availability of food and a low density of animals such that there is negligible competition for that food. These conditions are most closely approached when a population is in the early stage of active growth subsequent to the release of a nucleus of individuals into an area from which they were formerly absent. Figure 6.2 gives intrinsic rates of increase of several mammals, most of the data being gathered in that way. Alternatively the rate could be estimated from the initial stages of growth of a population recovering from overhunting. That would work for blue whales (*Balaenoptera musculus*) for example, which are presently recovering from intense overharvesting between about 1925 and 1955 (Cherfas 1988).

Intrinsic rate of increase r_m tends to vary with body size. The relationship has been calculated (Caughley and Krebs 1983; Sinclair 1996) for herbivorous mammals as:

$$r_m = 1.5W^{-0.36}$$

where W is mean adult live weight in kilograms. Table 6.1 gives r_m calculated by that equation for a range of body weights. In the absence of other data it provides an approximation that can be used to make a first estimate of sustained yield (see Chapter 19).

Fig. 6.2 Intrinsic rate of increase of mammals plotted against body weight. (After Caughley and Krebs 1983.)

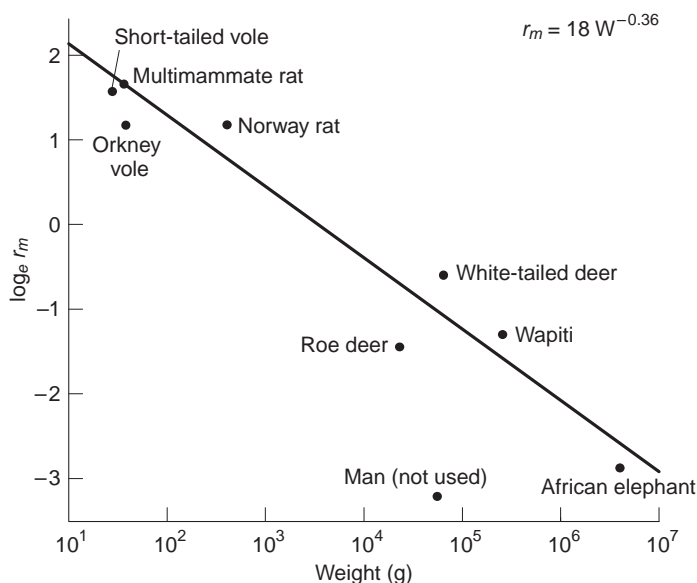


Table 6.1 Expected intrinsic rates of increase r_m on a yearly basis for herbivorous mammals as estimated from mean adult live weight.

Weight (kg)	r_m
1	1.50
10	0.65
100	0.29
1000	0.08

6.3 Fecundity rate

A population's rate of increase is determined by its size, by how many animals are born, and by how many die during a year. Hence, birth rate is an important component of population dynamics that can be measured in a number of ways. Of these the most useful is fecundity rate.

We measure fecundity rate as the number of female live births per female per unit of time (usually 1 year). That figure is often broken down into age classes to give a fecundity schedule as in Table 6.2, and each value is denoted m_x , female births per female in the age interval x to $x + 1$.

6.4 Mortality rate

The number of animals that die over a year is another important determinant of rate of increase, and again it can be measured in a number of ways. We measure it as the mortality rate, the number of animals that die during a unit of time (usually 1 year) divided by the number alive at the beginning of the time unit. As with fecundity, the rate is often given for each interval of age.

The pattern of mortality with age is summarized as a life table, which has a number of columns as in Table 6.3. The first is the age interval labeled by the age at the beginning of the interval and denoted x . The second is survivorship l_x , the probability at birth of surviving to age x . The third is mortality d_x , the probability at birth of dying in the age interval x , $x + 1$. The fourth, the most useful, is mortality rate q_x , the probability of an animal age x dying before the age of $x + 1$. The fifth,

Table 6.2 A fecundity schedule calculated for chamois.

Age (years) (x)	Sampled number (f_x)	Number pregnant or lactating (B_x)	Female births per female ($B_x/2f_x$) (m_x)
0	—	—	0.000
1	60	2	0.017
2	36	14	0.194
3	70	52	0.371
4	48	45	0.469
5	26	19	0.365
6	19	16	0.421
7	6	5	0.417
> 7	10	7	0.350

From Caughley (1970).

Table 6.3 Construction of a partial life table.

Age (years) (x)	Survival frequency (f_x)	Survivorship (l_x)	Mortality (d_x)	Mortality rate (q_x)
0	1200	1.00	0.58	0.58
1	500	0.42	0.17	0.40
2	300	0.25	0.08	0.32
3	200	0.17	—	—
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age-specific survivorship p_x is the probability at age x that an animal will still be alive on its next birthday.

Probabilities are estimated from proportions. The probability of a bird surviving to age x can be estimated for example by banding 1200 fledglings and recording the number still alive 1 year later, 2 years later, 3 years later, and so on. Let us say those frequencies were 500, 300, 200. Survivorship at age 0 (i.e. at birth) is $1200/1200 = 1$, by age 1 year it has dropped to $500/1200 = 0.42$, further to $300/1200 = 0.25$ at age 2 years, and further still to $200/1200 = 0.17$ at age 3 years.

No further data are needed to fill in the other columns corresponding to these values of l_x because each is a mathematical manipulation of the l_x column. Mortality d_x is calculated as $l_x - l_{x+1}$ ($1 - 0.42 = 0.58$ for $x = 0$ and $0.42 - 0.25 = 0.17$ for $x = 1$). Mortality rate q_x is calculated as $(l_x - l_{x+1})/l_x$ or d_x/l_x ($0.58/1 = 0.58$ for $x = 1$ and $0.17/0.42 = 0.40$ for $x = 2$). Table 6.3 shows the table fully constructed up to age 2 years, that for age 3 years being partial because data for age 4 years are needed to complete it. The subsequent rows would be filled in each year as the data became available.

So, constructing a life table is straightforward when the appropriate data are available. Pause for a moment to contemplate the difficulty of obtaining those data. Banding 1200 fledglings, or whatever number, poses no more than a problem in logistics. The difficulty comes in estimating what proportion of those birds are still alive at the end of the year. Nonetheless, there have been a number of direct studies of vital rates in wildlife species, based on mark-recapture methods (Lebreton *et al.* 1992; Gaillard *et al.* 2000).

Approximation methods are also available, based on age structure. If one can age a sample of the living population, or alternatively establish the ages at death of a sample of deaths from that population, an approximate life table can, in some circumstances, be constructed from those age frequencies.

6.5 Direct estimation of life-table parameters

There are basically two different ways in which life-table data can be directly estimated. The first, and rarest, method is to monitor the fates of all individuals in a relatively small population that is carefully studied over a long time. For example, virtually every young lion born to the population inhabiting the ecotone between the Serengeti plains and adjacent woodlands has been carefully monitored over the past three decades (Packer *et al.* 2005). The unique combination of facial spots, scars, and other features make it possible to visually recognize every individual and keep track of their fate. By collating data for each specific cohort, one can readily calculate the probability that any member born to this group survives to age x (the l_x series), by simply dividing the number of survivors at age x by the initial group size.

Even in this ideal situation, however, there are thorny problems associated with the estimation of life-table parameters. The difficult issue is that survival is like a game of chance: the outcome can vary considerably from one replicate to another (see Chapter 17). For example, a 0.5 probability of survival for an initial group of four individuals can lead to no survivors (expected 6.3% of the time), one survivor (expected 25% of the time), two survivors (expected 37.5% of the time), three survivors (expected 25% of the time), or even four individuals (expected 6.3% of the time). So the fact that two out of four individuals in a cohort survive over a given year does not conclusively demonstrate that the probability of survival really is 0.5, nor does the observation of no individuals surviving provide conclusive evidence against such a rate. As a result of the inherently variable nature of demographic processes, it is difficult to ascribe a particular risk of mortality with high likelihood, unless very large numbers of individuals are involved or such observations are repeated over many years.

The second way to estimate life-table parameters directly is to mark a large number of individuals at time t (A_t), then recover some of those individuals (b_{t+1}) in a subsequent sampling session, say a year later, to estimate the probability of survival. Marked individuals might be equipped with leg bands (as in many bird studies), ear-tags (as in many studies of small mammals), or even radiotransmitters (as in many studies of large mammals). If the true number of survivors is B_{t+1} , then the number of marked animals in the sample (b_{t+1}) depends on the detectability of individuals in each sample (c), typically under the presumption that $b_{t+1} = cB_{t+1}$. In this situation, not only is there stochastic variation to contend with, but also sample variation associated with detectability of individuals in the population. By chance, we might detect a relatively large number of marked individuals in a subsequent sample, for reasons wholly unrelated to survival probability.

The confidence we ascribe to survival probabilities estimated using these mark–recapture techniques depends critically on sample size, probability of recapture if an animal is still alive, mobility of marked animals and their loyalty to the site at which originally caught, the number of replicate sampling intervals, and whether or not newly marked animals have been repeatedly added to the population or not (Lebreton *et al.* 1992; Nichols 1992). Over the past two decades, there has been a revolution of sorts in the analysis of mark–recapture data, using sophisticated

computer programs, such as *SURGE* (Lebreton *et al.* 1992) or *MARK* (White and Burnham 1999). Many of these programs are available free of charge from the World Wide Web. We point interested readers to the encyclopedic review of demographic methodology by Williams *et al.* (2002) for an insightful discussion of different mark–recapture approaches and their statistical analysis.

Sophisticated mark–recapture experiments to estimate demographic parameters often involve comparisons among a large number of competing models (does survival vary among sexes, over time, across age groups, or between sites?). As we discuss in Chapter 15, such comparisons often require use of information–theoretic approaches to identify the most parsimonious model to explain a given data set. Recent versions of demographic analysis software, such as *MARK*, commonly include formal means of making choices among competing models (commonly either via Akaike’s information criterion (AIC) optimization evaluation or likelihood-ratio testing).

6.6 Indirect estimation of life-table parameters

If certain conditions (see the end of this section) are met, the age distribution of the living population can be used as a surrogate for the survival frequency f_x of Table 6.3 to produce an approximate life table. Many of the bovids can be aged from annual growth rings on the horns; some species of deer, seals, and possums produce growth layers in the teeth; and fish form growth lines on the scales. Unbiased samples of animals which have died from natural causes or from the live population yield data that may be amenable to life-table analysis.

It is sometimes possible to estimate the life table from a sample of individuals taken indiscriminately from the live population. This is most often derived from hunting statistics, although the reliability of such measures is often questionable, given the tendency for most hunters to select bigger or older animals. It is better to rely on catastrophic events that indiscriminately sample a cross-section of individuals in the population.

Flash floods during the autumn of 1984 killed thousands of woodland caribou from the George River herd in northern Quebec as they were migrating to their winter range. A large number of carcasses from this freak event washed up on the banks of the Caniapiscou River, where wildlife biologists working with the Quebec government retrieved them (Messier *et al.* 1988). The resulting sample of 875 female caribou 1 year of age and older was assumed to reflect the standing age composition of the living population. The frequency of newborns was estimated from calf–mother counts on the calving grounds.

If any study population is unchanging (termed “stationary”), the standing age distribution reflects survival frequencies by age. In the case of the George River caribou herd, however, a series of censuses were available showing strong evidence of exponential increase over the previous two decades, with $r = 0.11$ (Fig. 6.1). This introduces a bias into life-table parameter estimation, because older animals were born into a much smaller population than were younger individuals. The appropriate way to cope with this bias is to transform the age frequency data before deriving the life table. Table 6.4 demonstrates how to transform the age structure data, by multiplying the observed frequency at age x (f_x) by a coefficient (e^{rx}), that corrects for the bias in observed age frequencies caused by population growth.

One often needs to further smooth the age frequency data, especially when the data come from a relatively small sample of animals, to guarantee a continual decline in frequency with each successive age group. This is usually done by fitting a

Table 6.4 Life table for female caribou in the George River herd. Column 2 gives the original data from dead animals. Column 4 corrects column 2 by multiplying by e^{rx} , and column 4 smooths column 3.

Age	Frequency	Corrected frequency	Smoothed frequency	l_x	d_x	p_x	q_x	m_x
0	236.1	236.1	236.1	1.000	0.286	0.286	0.714	0
1	138	154.0	168.5	0.714	0.007	0.010	0.990	0
2	156	194.4	167.0	0.707	0.017	0.024	0.976	0.06
3	113	157.2	163.0	0.690	0.027	0.039	0.961	0.35
4	94	145.9	156.6	0.663	0.037	0.056	0.944	0.4
5	83	143.9	147.9	0.626	0.044	0.070	0.930	0.4
6	65	125.8	137.3	0.582	0.053	0.091	0.909	0.4
7	63	136.1	125.0	0.529	0.057	0.108	0.892	0.4
8	57	137.4	111.4	0.472	0.063	0.133	0.867	0.4
9	40	107.6	96.6	0.409	0.065	0.159	0.841	0.4
10	24	72.1	81.2	0.344	0.067	0.195	0.805	0.4
11	18	60.4	65.4	0.277	0.067	0.242	0.758	0.4
12	12	44.9	49.5	0.210	0.066	0.314	0.686	0.4
13	7	29.2	33.9	0.144	0.064	0.444	0.556	0.4
14	1	4.7	18.8	0.080	0.061	0.763	0.238	0.4
15	4	20.8	4.4	0.019	0.019	1.000	0.000	0.4

From Messier *et al.* (1988).

quadratic or cubic curve to the age distribution, using the values derived from the curve in place of the actual observations, as demonstrated for the George River caribou in Table 6.4. The survivorship series is then constructed by dividing each age frequency by 236, the d_x series as $l_x - l_{x+1}$, and the q_x series as d_x/l_x . If the age frequency data had not been smoothed, there would have been instances in which the observed frequency of an older age group exceeded that in the next youngest age group, implying survival rates exceeding 100%, an obvious impossibility.

An unbiased sample of ages at death due to natural causes, as might be obtained by a picked-up collection of skulls, may in some circumstances be treated as a multiple of the d_x series. Table 6.5 gives an example from African buffalo (Sinclair 1977). Only those skulls aged 2 years or older were counted because skulls from younger animals disintegrate quickly. These age frequencies are given in the second column of the table and total 183 skulls. The third column corrects for the missing younger frequencies: sample counts of juveniles in the field showed that the mortality rate over the first year of life was 48.5% and that 12.9% of the original cohort died in the second year. Hence, if the original cohort is taken as 1000, 485 of these would die in the first year of life and 129 in the second year. These values are tabled. They account for 614 of the original cohort, leaving 386 to die at older ages. The age frequencies of the 183 animals in the second column are thus each multiplied by 386/183 to complete the third column. The fourth column, d_x , is formed by dividing the fd_x frequencies by 1000 so that they sum to unity. Survivorship at age 0 (i.e. birth) is then set at one and the subsequent l_x values calculated by subtracting the corresponding d_x from each. Mortality rates q_x are calculated as before, as $q_x = d_x/l_x$.

The reliability of any life table developed indirectly from either a sample from the live population or a sample of animals that die of natural causes depends on how closely the data meet the underlying assumptions of the analysis:

Table 6.5 Construction of a life table from a pick-up sample of African buffalo skulls. The table is not corrected for rate of increase.

Age (x)	Mortality frequency (f_x)	Mortality corrected (fd_x)	Mortality (d_x)	Survivorship (l_x)	Mortality rate (q_x)
0	—	485	0.485	1.000	0.485
1	—	129	0.129	0.515	0.250
2	2	4	0.004	0.387	0.010
3	5	11	0.011	0.383	0.029
4	5	11	0.011	0.372	0.030
5	6	13	0.013	0.361	0.036
6	18	38	0.038	0.348	0.109
7	17	36	0.036	0.310	0.116
8	20	42	0.042	0.274	0.153
9	17	36	0.036	0.232	0.155
10	15	32	0.032	0.196	0.163
11	16	34	0.034	0.164	0.207
12	18	38	0.038	0.130	0.292
13	15	32	0.032	0.092	0.348
14	14	29	0.029	0.060	0.483
15	8	17	0.017	0.031	0.548
16	5	10	0.010	0.014	0.714
17	1	2	0.002	0.004	0.500
18	0	0	0.000	0.002	0.000
19	1	2	0.002	0.002	1.000
	183	1001	1.001		

1 The sample is an unbiased representation of the living age distribution in the first case or of the true frequency of ages at death in the second. The exercise would have to control the usual biases implicit in hunting activities if the sample of the living age distribution were obtained by shooting. One would be unlikely to use a sample obtained by sporting hunters, for example. The first age class is usually underestimated in a picked-up sample of ages at death because the skulls of young animals disintegrate much faster than do those of adults, thereby significantly biasing the table.

2 Age-specific fecundity and mortality must have remained essentially unchanged for a couple of generations.

3 Whether the sample is of the living population or of the ages at death, the population from which it came must have a rate of increase very close to zero, or else the data must be transformed to accommodate the observed rate of population change over the past two generations. Major fluctuations in recent rates of growth invalidate virtually all such indirect methods. This can limit the usefulness of such exercises in wildlife management.

6.7 Relationship between parameters

We restrict the following discussion to females for simplicity, but the points made apply also to the male segment of the population.

Remember that l_x is survivorship to age x , m_x is production of daughters per female at age x , and r is the exponential rate at which the population increases. Then:

$$\sum l_x m_x e^{-rx} = 1$$

which is the basic equation of population dynamics. If the survivorship and fecundity schedules hold constant, the population's age distribution will converge to the constant form of:

$$S_x = l_x e^{-rx}$$

which is called the **stable age distribution**. S_x is the number of females in a particular age class divided by the number of females in the first age class. The basic equation may thus be written $\sum S_x m_x = 1$. In the special case of rate of increase being zero, the stable age distribution, now called the **stationary age distribution**, is $S_x = l_x$ by virtue of $e^{-0x} = 1$. That is the justification for using such an age distribution to construct a life table. The stationary age distribution is the special case of the stable age distribution that obtains when $r = 0$. It has been argued that, since fecundity and mortality schedules seldom remain constant for long, the stable age distribution is little more than a mathematical abstraction, although a useful one. Although the stable distribution can be attained fairly quickly (roughly two generations) after mortality and fecundity patterns stabilize, most wildlife species that have been adequately studied have mortality and fecundity schedules that fluctuate, sometimes substantially, from year to year.

6.8 Geometric or exponential population growth

Thomas Malthus in 1798 recognized that populations have an intrinsic tendency towards exponential or geometric growth, just as a bank account at fixed interest grows geometrically with the amount of money in the account. The growth of such populations can be calculated as either a continuous or a discrete process. For simplicity, we will concentrate on discrete time representations of population growth. Strictly speaking, such models are most applicable to organisms whose patterns of deaths and births follow a seasonal or annual cycle of events, which includes most wildlife species. Consider, for example, a population whose finite growth rate (λ) is 0.61 and whose initial density (N_0) is 1.5. The geometric growth model predicts subsequent changes in density over time according to $N_t = N_0 \lambda^t$. The outcome depends on whether λ is larger or smaller than 1. When $\lambda < 1$ (Fig. 6.3) there is a decelerating pattern, while the outcome is changed to an accelerating pattern of growth when $\lambda > 1$ (Fig. 6.4).

Fig. 6.3 Population changes according to the geometric model with $\lambda = 0.61$.

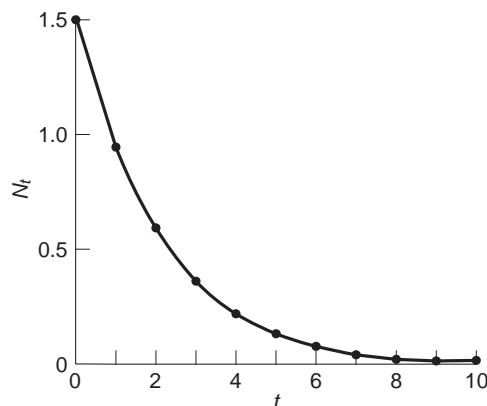
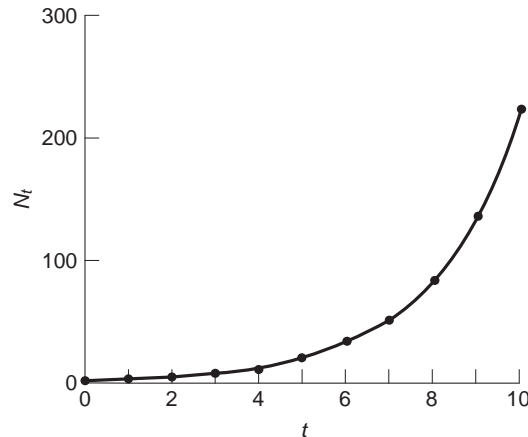


Fig. 6.4 Population changes according to the geometric model with $\lambda = 1.65$.



As we saw earlier in this chapter, the geometric model can be readily translated into the exponential model:

$$N_t = N_0 e^{rt}$$

Hence, it is straightforward to shift between representation of population dynamics in continuous time and discrete time. Such simple models are most appropriate for small populations introduced into a new environment or for a short period following a perturbation. For example, the George River caribou herd in eastern Canada grew exponentially at a rate of $r = 0.11$ during a 30-year period following recovery from overharvesting (Messier *et al.* 1988).

6.9 Summary

The dynamic behavior of a population – whether it increases, decreases, or remains stable – is determined by its age- or stage-specific mortality and fecundity rates interacting with the underlying distribution of ages or stages in the population. A wide variety of techniques are available for estimating age-specific parameters, summarized in the life table. When age-specific rates of fecundity and survivorship remain constant, the population's age distribution assumes a stable form, even though its size may be changing. These demographic parameters determine the rate of population change over time, forming the logical basis for many conservation and management decisions.

7 Dispersal, dispersion, and distribution

7.1 Introduction

This chapter explores some of the reasons why populations are found where they are. We describe the finer-scaled pattern as the dispersion and the broader scale as the distribution. We offer examples of how different factors such as temperature and seasonality limit the distribution of wildlife. We then discuss the causes for dispersal, and finally methods of modeling rates of dispersal of populations.

Dispersal is the movement an individual animal makes from its place of birth to the place where it reproduces. Dispersal is not to be confused with **migration** (movement backward and forward between summer and winter home ranges) or with **local movement** (movement within a home range). The terms immigration and emigration are used in mark–recapture studies to mean movement into and out of a study area of arbitrary size and location. Migration is used by population geneticists to mean “the movement of alleles between semi-isolated subpopulations, a process that by definition involves gene flow between subpopulations” (Chepko-Sade *et al.* 1987). Although these uses differ from their ecological uses, the difference is usually obvious from context and causes little confusion.

Dispersion is the pattern of spatial distribution taken up by the animals of an area. Dispersions may be fixed if the animals are sessile but more commonly they change with time under the influence of a changing dispersion of resources. A dispersion at a given time may be changed by dispersal, or local movement, or both.

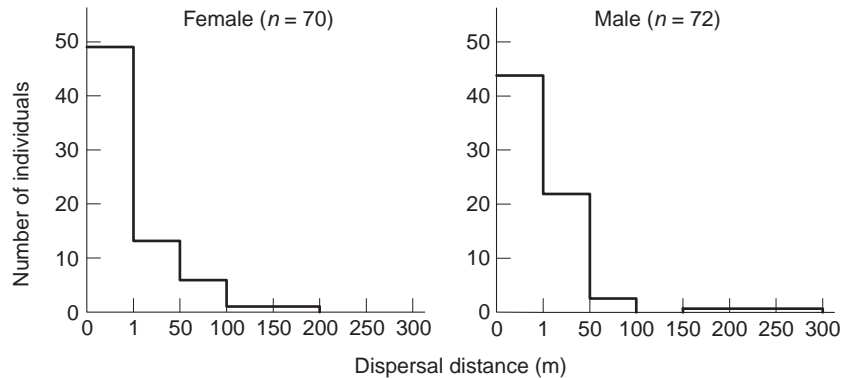
The **distribution** of a population or species is the area occupied by that population or species. It is depicted as the line drawn around the dispersion. The distribution can be subdivided into gross range and breeding range, and it can be mapped at different scales.

7.2 Dispersal

Dispersal is an action performed by an individual (Johnson and Gaines 1990). An animal disperses or it remains within its maternal home range. If it disperses, it may move only that distance sufficient to bring it to the nearest unoccupied and suitable area within which to establish its own home range, or it might move a considerable distance, crossing many areas that look suitable enough, before settling down.

The mechanism of dispersal may also vary. The individual may be pushed out of the maternal home range by a parent or it may move without any prompting save for that supplied by its genes. The young of some species never meet their parents (e.g. frogs, reptiles, the mound-building birds of the family Megapodidae) and so must provide their own motivation. In mammals, at least, there are two forms of dispersal that have been recognized (Stenseth and Lidicker 1992). **Presaturation** dispersal is seen in some species of small mammals where juveniles leave their natal range even when the density of the population is low. The mechanism is either that

Fig. 7.1 The frequency distributions of distances dispersed by juvenile rat kangaroos. (Data from Jones 1987.)



the juveniles leave voluntarily, their behavior being innately determined by their genes (e.g. in Belding's ground squirrels (*Spermophilus beldingi*); Holekamp 1986); or that adults forcibly exclude juveniles. **Saturation** dispersal is seen in many large mammals (Sinclair 1992). In this case dispersal occurs when a population reaches a threshold density determined by food limitation. Dispersal then is density dependent (see Chapter 8 for an explanation of this mechanism) so that population density remains the same on the initial area. Examples of this have been described for Himalayan tahr (*Hemitragus jemlahicus*) as they spread through the Southern Alps of New Zealand (Parkes and Tustin 1985), and for wood bison (*Bison bison*) as their population increased through their former range in the boreal forest of Canada (Larter *et al.* 2000) (see Section 7.6 for modeling range expansion).

The likelihood of dispersal differs markedly between individuals of a population. Figure 7.1 shows a sample of distances dispersed by juvenile kangaroo rats (*Dipodomys spectabilis*) (Jones 1987), a solitary, nocturnal, grain-eating desert rodent. Females averaged 29 m and males 66 m, but the majority of individuals did not disperse at all. Jones (1987) reported that adults of this species do not disperse much: 70% of adult males and 61% of adult females remained in one mound for the rest of their lives. Juvenile females of red deer (*Cervus elaphus*) seldom disperse but adopt home ranges that overlap those of their mothers. In contrast, males leave the natal home range between the ages of 2 and 3 years, mostly joining stag groups in the vicinity (Clutton-Brock *et al.* 1982).

Patterns of dispersal are related to the type of mating system (Greenwood 1980, 1983; Dobson 1982; Greenwood and Harvey 1982). Thus, in mammals, females are concerned with obtaining resources while males compete for mates. In general, males disperse in promiscuous and polygynous species because they are more likely to find new mates by doing so, while females are philopatric (i.e. remain at their birth site) because they are more likely to find food in areas they know well. Both sexes disperse in monogamous species. Amongst higher vertebrates, one sex is more prone to dispersal than the other. Thus, in mammals males are the dispersers whereas in birds it is the females which disperse, although there are exceptions for both groups. For example, in mammals females are the dispersers in wild dogs (*Lycaon pictus*) and zebra (*Equus burchelli*). In fishers (*Martes pennanti*) and wolves, both sexes disperse equally (Arthur *et al.* 1993; Boyd and Pletscher 1999).

The causes of dispersal fall into three broad categories: competition for mates, avoidance of inbreeding, and competition for resources (Johnson and Gaines 1990). In

polygynous species, females invest more in each offspring than do males, and so their reproductive success is determined by resource competition. Male reproductive success is limited by the number of mates they can find, so competition for mates is important.

Inbreeding avoidance is often cited as a cause of dispersal on theoretical grounds (reviewed in Thornhill (1993); see Section 17.3.5 for an explanation of the genetics of inbreeding depression). Inbreeding depression was observed in a captive wolf (*Canis lupus*) population (Laikre and Ryman 1991). In contrast, there was no evidence of inbreeding depression or avoidance in a social carnivore, the dwarf mongoose (*Helogale parvula*) (Keane *et al.* 1996). In general, the occurrence of inbreeding depression depends on the species (Waser 1996). There are some instances where inbreeding avoidance has been found, as in some species of birds (Pusey 1987; Keller *et al.* 1994), primates (Pusey 1992), rodents (Hoogland 1982), and marsupials (Cockburn *et al.* 1985). However, there are many instances where populations occur in small numbers, inbreeding is not avoided, and there is no deleterious effect of inbreeding (Keane *et al.* 1996). In other cases there are multiple causes of dispersal (Dobson and Jones 1985).

Dispersers tend to have lower survival than those that remain in their natal area. In arctic ground squirrels (*Spermophilus parryi*) survival of philopatric juveniles was 73%, whereas survival of dispersing squirrels was in the range 25–40%. Also, survival declines with the distance of dispersal due to the increasing probability of being caught by predators (Byrom and Krebs 1999). The survival of dispersing ferrets (*Mustela furo*) in New Zealand was 100% where predators had been removed experimentally compared with only 19–71% in areas where predators were present (Byrom 2002). However, survival of dispersing male San Joachin kit foxes (*Vulpes macrotis mutica*) was higher than that for philopatric males (Koopman *et al.* 2000), indicating exceptions to the rule.

7.3 Dispersion

Dispersions may be random, clumped, or spaced. The most common is a **clumped dispersion** (sometimes called a **contagious dispersion**). If the area is divided into quadrats and the frequency distribution of animals per quadrat is recorded, the variance of that distribution will equal its mean if the animals are randomly distributed (a Poisson distribution), the variance will be greater than the mean if the animals are clumped at that scale, and the variance will be less than the mean if the animals space themselves.

Scale is important when dispersions are considered because two or more orders of dispersion may be imposed upon each other: randomly distributed clumps of animals for example. In these circumstances a quadrat in a grid of small quadrats will include either part of a group or it will miss a group: its count will be of many animals or of no animals. When the grid comprises large quadrats, an average quadrat will contain several groups of animals and the variation in counts between quadrats will be less marked. The dispersion is the same whether the quadrats used to sample it are large or small, but in this case the clumping as measured by the variance/mean ratio will appear to be more intense when quadrats are small.

An alternative to characterizing dispersion in terms of the frequency distribution of quadrats containing 0, 1, 2, etc., animals per quadrat is instead to record the frequency distribution of nearest-neighbor distances or of the distances between randomly chosen points and the nearest animal to each. The problem of quadrat size

does not arise because no quadrats are involved, but no simple measure is presently available for distributions of distances that clearly differentiates classes of dispersions, one from the other, given the wealth of possible dispersions. However, J.M. Cullen and M. Bulmer (in Patterson 1965) provide a formula for calculating the random distribution of inter-individual (or intergroup) distances in a known area. Given the same number of individuals N , distributed randomly with respect to each other in the same area A , then the proportion (p) of individuals having their nearest neighbor at a distance x is given by the expression:

$$p_x = \exp[-(\pi N/A)(x - 0.5a)^2] - \exp[-(\pi N/A)(x + 0.5a)^2]$$

where a is the unit of measurement used. The number at distance x is Np_x . Thus, if one observes 200 birds in an area of 2 km radius ($A = 12.57 \times 10^6 \text{ m}^2$), and observations are in units of 50 m ($= a$), then the expected frequency of distances at the nearest interval ($x_1 = 25 \text{ m}$) is 23.5, that at the next interval ($x_2 = 75 \text{ m}$) is 55.2, and so on until the sum of Np_x equals 200. We see that the increments of x must start with the first one equal to $0.5a$ (midpoint of the first interval) and then increase in increments of a (thus 25, 75, 125, 175, etc.). By comparing this frequency of distances with the observed frequency one can identify clumped or overdispersed distributions.

Dispersion is affected by the **home range** of individuals, that is the area used during the normal daily activities. Traditionally, home ranges are estimated from radiotelemetry locations (usually > 30 locations are required) using computer software packages. Habitat type affects range area (Relyea *et al.* 2000), as does the gender of the individual (McCullough *et al.* 2000). Some species have tight habitat preferences, their dispersion reflecting where that habitat is to be found. Others are more catholic in their requirements and will therefore be distributed more evenly across the landscape. The ecology of the dispersion is important. Dispersion can be measured more directly, however, by the average distance between locations (Conner and Leopold 2001). We considered the concept of home range in Chapter 5, in which we outline methods of determining the key determinants of home range use.

When we design surveys to count wildlife (see Chapter 13) we have to pay attention to its dispersion and allocate our sampling units accordingly. We explore this practical aspect of dispersion more fully in Section 13.4.

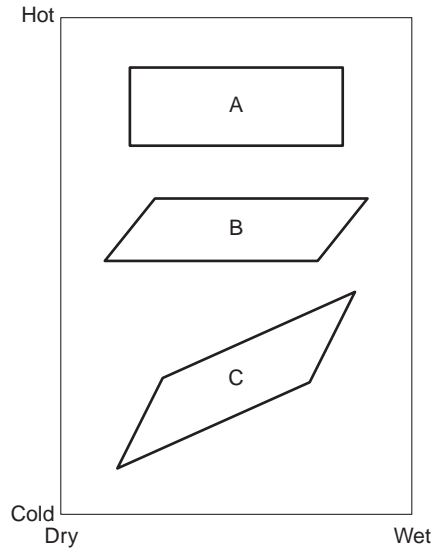
7.4 Distribution

Krebs (2001) considered that “the simplest ecological question one can ask is simply: Why are organisms of a particular species present in some places and absent in others?” There are several interesting ways that this question can be answered. We start with a consideration of the ultimate limits of a species’ range, before going on to consider the distribution of introduced or invading species and finally to consider patterns of occupancy in spatially subdivided populations (metapopulations).

Figure 7.2 shows three hypothetical distributions, not as a map but as a plot within a range of mean annual temperature and mean annual rainfall. For species A, temperature and rainfall act independently of each other in setting limits to distribution. A single mean temperature and a single mean annual rainfall is all one needs to predict whether or not the species will be in a given area.

The distribution of species B is also determined by temperature and rainfall but this time in an asymmetric interactive manner. Distribution is determined absolutely

Fig. 7.2 Three hypothetical envelopes of adaptability of a species to temperature and moisture: A, the two factors act independently; B, the level of one factor influences the effect of the other; C, the effect of each factor varies according to the level of the other. (After Caughley *et al.* 1988.)



by an upper and lower limiting temperature but it is demarcated within those bounds by rainfall whose effect varies with temperature. High rainfall is tolerated only in hot areas and low rainfall only in colder areas where evaporation is reduced.

The distribution of species C is controlled by a symmetric interaction of rainfall and temperature. The species' tolerance of high temperatures increases with increasing annual rainfall, and the tolerance of the species to rainfall increases with temperature. This is a two-way interaction.

A known range of tolerance to one or more factors like temperature and rainfall does not translate directly into a map of distribution because the factors may interact as in example B and C of Fig. 7.2, the level of one factor determining the effect of another. Whether distribution is determined by one or several factors depends critically on the geographic dispersion of the levels of each factor.

7.4.1 Range limited by temperature

Temperature can limit the distribution of animals through direct effects on their physiology and indirectly by affecting resources. Some distributions can be described empirically by temperature contours (isotherms). Thus, the southern limit to northern hemisphere seals is set by sea surface temperatures never exceeding 20°C (Lavigne *et al.* 1989). The reason is unclear, but most seals breed in regions of high marine productivity and these are largely restricted to high latitudes. Similarly, the penguins of the southern hemisphere inhabit seas with temperatures lower than 23°C. Most penguin species inhabit latitudes between 45°S and 58°S where marine productivity is high (Stonehouse 1967). They reach the equator at the Galapagos Islands off the Pacific coast of South America, but only because those shores are bathed by the cold Humboldt current.

The northern limit for rabbits (*Oryctolagus cuniculus*) in Australia is marked by the 27°C isotherm. These temperatures coincide with high humidity, and the combination of the two causes resorption of embryos so that the animals cannot breed.

Cold is clearly an important factor limiting species in the Arctic and subarctic. Although the Arctic is an important breeding ground for birds, most leave during

winter. Only four North American species can withstand the cold to reside year round in the Arctic: the raven (*Corvus corax*), the rock ptarmigan (*Lagopus mutus*), the snowy owl (*Nyctea scandiaca*), and the hoary redpoll (*Acanthis hornimanni*) (Lavigne *et al.* 1989). Amphibians and reptiles are particularly affected by temperature. The American alligator (*Alligator mississippiensis*) cannot tolerate temperatures below 5°C. Although several species of amphibians and reptiles tolerate freezing temperatures, in general there is a negative relationship between the number of species and the latitude. The direct effect of cold in limiting the distribution of these groups is probably less important than the availability of hibernation sites remaining above lethal temperatures (Lavigne *et al.* 1989).

Movements of large mammals can be affected by temperature. In the Rocky Mountains several ungulates, such as moose (*Alces alces*), elk, and deer, move down hill for the winter. Sometimes a temperature inversion in winter positions a warmer air layer above a colder one, and in these conditions Dall sheep (*Ovis dalli*) in the Yukon climb higher rather than lower.

The limiting effects of temperature are demonstrated by changes in the range of several species during historic times. Temperatures increased in the northern hemisphere between 1880 and 1950. The breeding ranges of herring and black-headed gulls (*Larus argentatus*, *L. ridibundus*) moved north into Iceland, and that of green woodpeckers (*Picus viridis*) extended into Scotland. Temperatures have declined since 1950 and the breeding ranges of snowy owls and ospreys (*Pandion haliaetus*) have moved south (Davis 1986). On the American prairies the warming period was associated with severe droughts in the 1930s. As a result the cotton rat (*Sigmodon hispidus*) has spread north (Davis 1986). Further changes in the distribution of these and many other wildlife species are expected in the future, as a result of global warming.

Cold temperatures themselves may be less important than the consequent changes in snow pack. Caribou must expend greater amounts of energy in exposing ground lichens when snow develops a crust (Fancy and White 1985). Even further north on Canada's High Arctic Islands the warming temperatures of spring melt the surface snow. As the water trickles through the snow pack it freezes when it hits the frozen ground and forms an impenetrable layer. The caribou abandon feeding in those areas and may migrate across the sea ice to areas where the wind has blown the shallow snow away (Miller *et al.* 1982).

Deep snow limits other species also. North American mountain sheep (*Ovis canadensis*, *O. dalli*) are usually found in winter on cold windswept ledges where there is little snow. Deer (*Odocoileus* species) are limited by snow cover of moderate depths (< 60 cm) whereas moose can walk through meter-deep snow (Kelsall and Prescott 1971). Both move to coniferous forest in late winter because the snow is less deep there (Telfer 1970; Rolley and Keith 1980).

The stress of cold temperature has resulted in various adaptations to conserve energy, the most notable being the hibernation of ground squirrels during winter and the dormancy and lowering of body temperature of bears. Hummingbirds also lower body temperature overnight to about 15°C or when resting in cold conditions, a state called **torpor**. The limiting effect of temperature on ground squirrels operates indirectly through soil type, slope, and aspect. Squirrels need to dig burrows deep enough to avoid the cold and this requires sandy, friable soil. They also need to avoid being swamped by melt water in spring, so burrows are situated on slopes where water can drain away. Similarly, in Australia, the distribution of rabbits within the 27°C isotherm is

7.4.2 Range limited by water loss and heat stress

influenced by soil type, soil fertility, vegetation cover, and distribution of water (Parer 1987).

High temperatures are often combined with high solar radiation and restricted water supplies. In high-rainfall areas the last factor is important for restricting distribution; in arid regions all three have interrelated effects on animals. These effects are expressed as heat loads built up in the body, and there are various adaptations to overcome them.

Adaptations to high temperatures include behavioral responses such as using shade in the middle of the day and restricting feeding to the hours of darkness. Both eland (*Taurotragus oryx*) and impala (*Aepyceros melampus*) reduce heat stress by feeding at night in East Africa (Taylor 1968a). At the driest times of year both species boost water intake by switching from grazing grasses and forbs to browsing on succulent shrubs (Taylor 1969; Jarman 1973).

Solar radiation restricts the movements of animals that are large and that have dark coats. Elephant and buffalo are examples where they seek shade in the heat of the day to cool off (Sinclair 1977). Coat color and structure can reduce heat loads. The lighter tan-colored coat of hartebeest (*Alcelaphus buselaphus*) reflects 42% of short-wave solar radiation as against only 22% for the darker coat of eland. In both species re-radiation of long-wave thermal radiation is greater than that absorbed, and this represented 75% of total heat loss (Finch 1972).

High heat loads can be avoided by sweating when water is abundant. African buffalo, eland, and waterbuck use sweating for evaporative cooling (Taylor 1968a; Taylor *et al.* 1969b). Buffalo keep body temperature in the range 37.4–39.3°C and allow body temperature to rise to 40°C only when water is restricted. They cannot reduce water loss from sweating when water is restricted (Taylor 1970a,b). Waterbuck show similar physiological adaptations. When water is restricted for 12 hours at 40°C ambient (environmental) temperature they lose 12% of their body weight compared with the 2% for beisa oryx (*Oryx beisa*) which is a desert-adapted species (Taylor *et al.* 1969b). As a consequence both buffalo and waterbuck must remain within a day's walk of surface water.

Large animals can afford to lose water by sweating but smaller animals such as the gazelles cannot. They employ panting instead, as do species in arid areas (e.g. the beisa oryx) or species on open plains with high solar radiation, such as wildebeest (Robertshaw and Taylor 1969; Taylor *et al.* 1969a; Maloiy 1973).

Some species can adapt to extreme arid conditions by allowing their body temperature to rise before they start panting; up to 43°C for Thomson's gazelle (*Gazella thomsonii*) and 46°C for Grant's gazelle (*G. granti*) (Taylor 1972). Other adaptations for water conservation include restriction of urine output, concentrating the urine, and reabsorbing water from the feces. Dikdik, a very small antelope that lives in semi-arid scrub away from water, had the lowest fecal water content and the highest urine concentration of all antelopes, followed by hartebeest, impala, and eland (Maloiy 1973).

Grazing ungulates in Africa are restricted to areas within reach of surface water and all show behavioral adaptations such as night feeding or migration (Sinclair 1983). Those that can do without water are all browsers (Western 1975). Beisa oryx and Grant's gazelle select hygroscopic shrubs (*Disperma* species). They eat them at night because these shrubs contain only 1% free water in the day but absorb water from the air at night to boost the water content of the leaves to 43% (Taylor 1968b).

Perhaps not apparent at first sight is the restricted availability of water for wildlife in cold regions. Not only are many of those regions deserts, as their rainfall is low, but during winter the moisture is available only as snow, and valuable energy is needed to melt it. Arctic mammals go to some lengths to conserve water. Caribou recycle nitrogen to reduce the formation of urine, thereby conserving water.

7.4.3 *Range limited by day length and seasonality*

The distribution of many North American birds is limited at northern latitudes by season length, the number of days available for breeding above a certain temperature. This is another aspect of temperature limitation. However, the southern boundary is limited by day length, the number of hours available for feeding themselves and their young (Emlen *et al.* 1986; Root 1988).

Seasons are highly predictable in the northern temperate latitudes of North America and Eurasia, and many birds and mammals have evolved a response to **proximate factors** (i.e. the immediate factors affecting an animal), particularly day length (photoperiod), which trigger conception and result in the production of young during optimum conditions. Such conditions are the **ultimate factors** (i.e. the underlying selection pressure) to which an animal is adapted by breeding seasonally (Baker 1938).

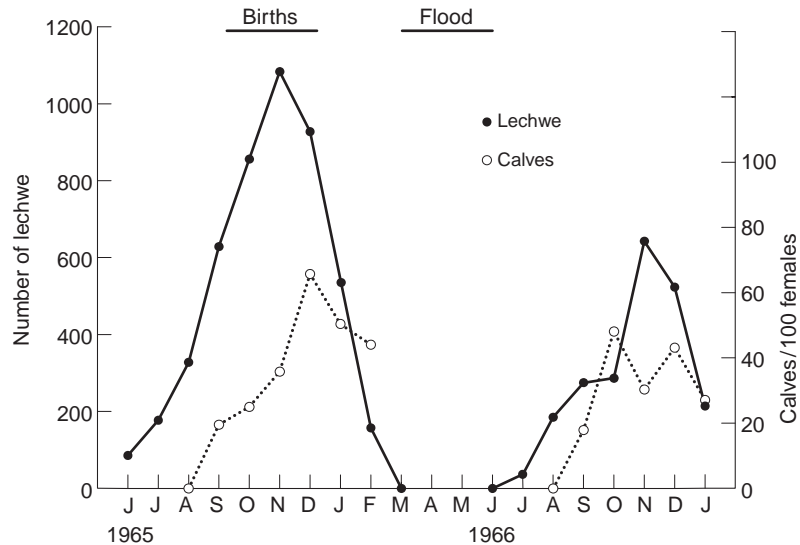
Increasing photoperiod determines the start of the breeding season in many bird species (Perrins 1970), while declining photoperiod triggers the rut in caribou; the rut is so synchronized that most conceptions occur in a mere 10-day period starting around the first day of November (Leader-Williams 1988). Moose and elk also have highly synchronized birth seasons (Houston 1982), which suggests photoperiodic control of reproduction.

Among tropical ungulates only the wildebeest is known to respond to photoperiod. In southern Africa it uses solar photoperiod to synchronize conceptions, but near the equator where solar photoperiod varies by only 20 minutes in the year it is cued by a combination of lunar and solar photoperiod (Spinage 1973; Sinclair 1977).

In variable environments with less predictable seasons, as in the tropics and arid regions, animals tend not to use photoperiod to anticipate conditions but rather adjust their reproductive behavior to the current conditions. Thus, tropical birds begin breeding when the rainy season starts, responding to the increase in insect food supply and the growth spurt of the vegetation (Sinclair 1978). In some arid areas such as Western Australia the seasonality of rain is relatively predictable but its location is not. Emus (*Dromaius novaehollandiae*) there travel long distances searching for areas that have received rain (Davies 1976), as do male red kangaroos (*Macropus rufus*) (Norbury *et al.* 1994).

Most ungulates produce their young during the wet season in Africa and South America, but put on fat before giving birth. This fat is then used during lactation, the period when the energy demands on the female are highest (Ojasti 1983; Sinclair 1983). Therefore, nutrition in the seasonal tropics becomes both the proximate and ultimate factor determining the timing of births. An example is provided by the lechwe (*Kobus lechwe*), an African antelope that lives on seasonally flooded riverine grasslands (Fig. 7.3). During the peak of the floods animals are confined to the less preferred surrounding woodlands. The greatest area of flood plain is exposed at the low point in the flood cycle and it is at this time, corresponding with greatest availability of food, that births take place. In Zambia the peak of births occurs in the dry season 3 months after the rains; in the Okavango swamp of Botswana it occurs in

Fig. 7.3 The numbers of lechwe, a flood plains antelope of southern Africa (●, left axis), increase on the flood plains as water recedes in the Chobe River exposing the greatest area of high-quality food. The recruitment of newborn per 100 females (○, right axis) shows that births occur at this time. (After Sinclair 1983, which is after Child and von Richter 1969.)



the middle of the wet season 9 months after the previous rains; but both occur when the swamp grasslands are most available.

7.4.4 Range limited by biotic factors

So far we have discussed range limitation by abiotic environmental factors. However, these abiotic factors can interact with biotic processes such as predation and competition to further limit a species' range. For example, the geographic distribution of arctic fox (*Alopex lagopus*) is largely in the tundra of the Holarctic and is separate from that of the more southerly red fox (*Vulpes vulpes*). However, their ranges overlap in some areas of North America and Eurasia. The northern limit of the red fox's range is determined directly by resource availability, which is determined by climate. The southern limit of the arctic fox's range is determined by interspecific competition with the more dominant red fox (Hersteinsson and Macdonald 1992).

7.5 Distribution, abundance, and range collapse

A major pattern in ecology is the positive relationship between the range of a species and its abundance. In general, locally abundant species have wide ranges whereas rare species have narrow ranges (Brown 1995; Gaston and Blackburn 2000). This observation has led to Rapoport's rule, namely that the latitudinal extent of a species' range increases towards the poles (Rapoport 1982). This general pattern is modified by species richness, rainfall, vegetation, and land surface as seen in studies of birds (Gentilli 1992) and mammals (Pagel *et al.* 1991; Letcher and Harvey 1994; Smith *et al.* 1994).

Of great importance in conservation management is what happens to a species' range when the population declines. One expects that population densities tend to be higher at the center of a population's range than at the periphery. Geographic ranges should collapse from the outside, with the center being the last to go (Brown 1995). Analyses of range contractions in a wide variety of animals and plants suggest that populations often collapse first in the center, leaving isolated fragments on the periphery (Lomolino and Channell 1995; Channell and Lomolino 2000). These collapses were due to the variety of causes outlined by Caughley (1994). Thus, peripheral populations not only provide a refuge for endangered species but also represent genetic

and morphological varieties that differ from central populations (Lesica and Allendorf 1995).

7.6 Species reintroductions or invasions

Many species of wildlife have been eliminated from their traditional range, for one reason or another. This can even happen to common species, like the plains bison (*Bison bison*). Europeans arriving in North America encountered millions of bison on the Great Plains. In remarkably short order, this massive population was nearly extirpated, through a combination of commercial hunting by Europeans and subsistence hunting by aboriginal groups, competition with livestock, and fencing off of migration routes (Isenberg 2000). Since the turn of the century, the plains bison has been re-established by wildlife authorities to parts of its former range, though in nothing like its former abundance. Such reintroductions are becoming ever more common.

In other cases, species have naturally recovered from catastrophic decline, expanding into their former range. A well-documented example is the California sea otter *Enhydra lutris* (Lubina and Levin 1988). This species was nearly exterminated throughout its Pacific coast range through overharvesting by fur traders in the late nineteenth century, before a moratorium on harvesting was signed in 1911. A small relict population of otters survived in an inaccessible part of the California coast south of Monterey Bay. This small population provided the nucleus for gradual spread of the population both northwards and southwards along the coast.

Whether intentional or accidental, such reintroductions have some fascinating characteristics that have important bearing on their successful conservation. Key among these is the interplay between demography and patterns of movement.

7.6.1 Diffusive spread of reintroduced species

Although there are many elegant ways to model patterns of movement by invasive or reintroduced species (Turchin 1998), simple random walk models can often predict the pattern of spread surprisingly well. We first consider what is meant by a random walk, then use this algorithm to develop a simple model of population distribution.

What pattern would emerge over time, for a single individual that moves randomly every day of its life? We will assume that this hypothetical animal can only move forwards, backwards, or sideways, one step at a time. We further assume that each of these events is as probable as remaining where it is. To model this, we need to sample randomly from a uniform probability distribution (see Box 7.1).

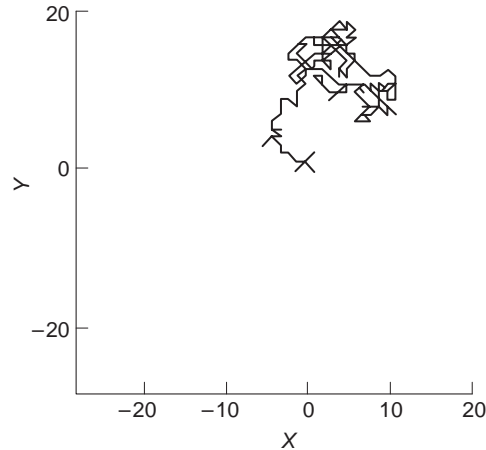
Box 7.1 Modeling a random walk in space.

We first need to randomly sample a large number of values uniformly distributed between 0 and 1, assigning each random number on this interval to either the variable p or the variable q . We then use these probabilities to mimic forwards versus backwards movement using the variable x and side-to-side movements using the variable y , using the logic shown below. As a result of this logic, an animal would move left one-third of the time, right one-third of the time, and stay on track one-third of the time. Similar probabilities correspond to forwards, backwards, and stationary outcomes.

$$x_{t+1} = \begin{cases} x_t - 1 & \text{if } P_t < 0.333 \\ x_t + 1 & \text{if } P_t > 0.333 \wedge P_t < 0.667 \\ x_t & \text{otherwise} \end{cases}$$

$$y_{t+1} = \begin{cases} y_t - 1 & \text{if } q_t < 0.333 \\ y_t + 1 & \text{if } q_t > 0.333 \wedge q_t < 0.667 \\ y_t & \text{otherwise} \end{cases}$$

Fig. 7.4 Hypothetical trajectory over 100 time steps for a single individual following a random walk, starting from the origin (0,0).



For this kind of random walk model, most trajectories tend to find their way back to a position not far from the initial starting point (Fig. 7.4). In other words, walking randomly is not a very effective means of getting anywhere new. This is a useful null model, however, that sets an extreme standard against which we might evaluate the movements of real organisms. The random walk model is perhaps most plausible at large spatial scales, such as for dispersing juveniles, in which animals have no past experience with local conditions.

We can readily expand this kind of model to a group of individuals (Case 2000). To keep it simple, we will concentrate on only one spatial dimension, such as for sea otters dispersing up and down the coast of California. Let's say that there are 100 individuals released at a central position "0" and that each individual has a 20% probability of moving left and a 20% probability of moving right, with position along this axis indicated by the variable x . This probability we will term " d " for dispersal. Local changes in density of individuals can be modeled in the following manner:

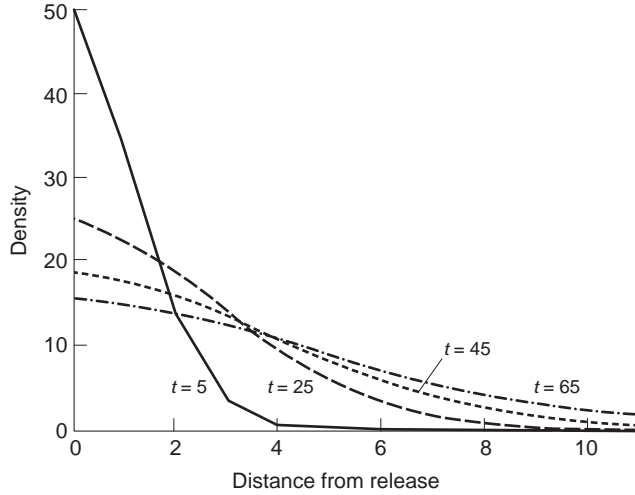
$$N_{x,t+1} = N_{x,t} - 2dN_{x,t} + dN_{x-1,t} + dN_{x+1,t}$$

The local population loses $2 \times d \times N$ individuals due to movement in either direction, but gains $d \times N$ individuals from each adjacent site. We need to repeat this exercise over the full range of distance intervals.

The output of this model demonstrates two important features (Fig. 7.5). First, the spatial distribution of individuals in the population begins to take on a bell-shaped or normal distribution over time. Second, the rate of spread is initially fast, but slows over time. This is because movement away from the release point is balanced to a considerable degree by movement backwards. This slower movement away becomes more pronounced over time because the distribution is getting flatter. When dynamics are driven purely by random motion the population range spreads at a rate proportional to $\sqrt{\text{time}}$. If we repeat this simulation with a larger fraction of dispersers (say $d = 0.3$), the rate of spread will increase accordingly. The rate of spread is proportional to \sqrt{d} .

We can use our random walk model to derive the differential equation that defines diffusive changes in local density, over a continuous gradient of space and time:

Fig. 7.5 Variation in the population density of individuals over time, when those individuals redistribute themselves every time step (t) according to an unbiased random walk.



$$\Delta N_x = N_{x,t+1} - N_{x,t} = -2dN_{x,t} + dN_{x-1,t} + dN_{x+1,t}$$

We then rearrange terms on the right-hand side of the equation:

$$\Delta N_x = d[(N_{x-1,t} - N_{x,t}) - (N_{x,t} - N_{x+1,t})]$$

The rate that individuals accumulate at site x depends on the degree of difference between the density gradient below the site and the density gradient above the site. In other words, it is not the gradient itself, but the rate of change of the density gradient over space that dictates the rate of diffusive movement. Mathematicians refer to the rate of change of the density gradient as the second derivative. If this occurs over short enough intervals of time and space, then the result is the following differential equation (called the diffusion equation in one dimension):

$$\frac{dN(x, t)}{dt} = D \frac{\partial^2}{\partial x^2} N(x, t)$$

The solution to this equation is the normal distribution:

$$N(x, t) = \frac{N_0}{\sqrt{4\pi Dt}} \exp\left[-\frac{(x - \mu)^2}{4Dt}\right]$$

where t is the time since the animals were released, μ is the initial position (usually 0), and D is the diffusion coefficient. It reflects how fast individuals tend to diffuse away from an initial point of release. We discuss how to calculate it below. This equation may look familiar – it is closely related to the normal (sometimes called Gaussian) probability distribution. The variance in spatial locations is given by $\sigma^2 = 2Dt$.

The easiest way to estimate the diffusion coefficient D is to estimate the mean-squared displacement of the individuals in the population over time. One simply measures the distance of a given individual from its original release point, squares that displacement to get rid of positive versus negative values, sums the squared

displacements for all individuals, and divides this sum by the total sample size to estimate mean-squared displacement. D is then calculated by dividing mean-squared displacement by $2t$.

In the more typical case of diffusion in two dimensions (x and y , centered at the release point), these equations are slightly altered:

$$\frac{dN(x, y, t)}{dt} = D \left[\frac{\partial^2}{\partial x^2} N(x, y, t) + \frac{\partial^2}{\partial y^2} N(x, y, t) \right]$$

$$N(r, t) = \frac{N_0}{4\pi Dt} \exp\left(-\frac{r^2}{4Dt}\right)$$

where r is the distance (i.e. radius) from the release point. Despite the slight change in formula, this equation also predicts that the range occupied by the population is proportional to $\sqrt{\text{time}}$. This is a very useful prediction that differs from other models of population spread, as we shall shortly see.

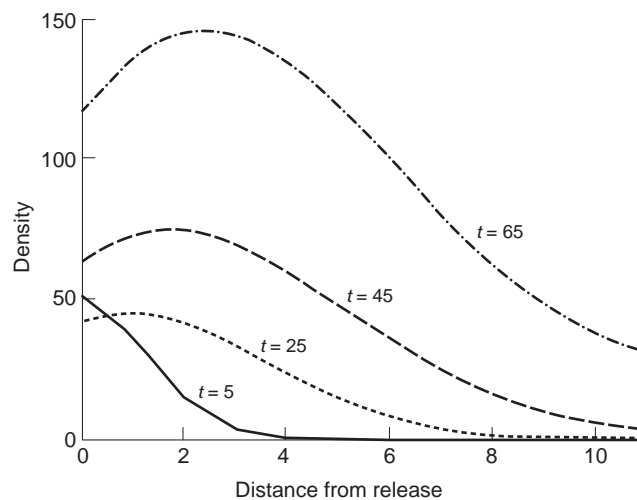
7.6.2 Spread of reintroduced species: diffusion + exponential growth

As we discussed in Chapter 6, a newly reintroduced population is likely to have plenty of resources with which to grow and multiply. This logically leads to geometric or exponential growth, at least in the initial period following release. Unrestricted population growth can be readily incorporated in our random walk model of population spread. We simply multiply the local population by the finite rate of growth λ (in this case, let us say that $\lambda = 1.05$):

$$N_{x,t+1} = \lambda N_{x,t} - 2dN_{x,t} + dN_{x-1,t} + dN_{x+1,t}$$

The rate of spread now seems to be much more consistent over time (Fig. 7.6) than was the case for diffusive movement alone (Fig. 7.5). In fact, the population range now spreads at a rate proportional to t and d because the population grows fastest where density is highest. This relationship tends to create a rapid rate of change in

Fig. 7.6 Variation in the population density of individuals over time, when those individuals redistribute themselves every time step (t) according to an unbiased random walk. Unlike Fig. 7.5, the population is also growing at an annual rate of $\lambda = 1.05$.



the density gradient, which we have already suggested fuels a high rate of diffusion. The net result is a population that explodes over both time and space.

Another interesting feature of the diffusion + exponential growth model is that a standing wave of animals spreads over time across the landscape (Fig. 7.6), rather than the gradually eroding “mountain” seen in the pure diffusion model (Fig. 7.5). This wavelike form of spread is echoed in most models that incorporate population growth as well as diffusive movement, such as those with logistic growth or predator–prey models. The velocity with which this wave rolls across the landscape is identical in virtually all such models: $v = 2\sqrt{(\lambda D)}$.

7.6.3 Empirical tests of diffusion theory

We should be able to discriminate between alternative models of population spread by looking at population range versus time. If the rate of increase of the radius of population distribution becomes less over time, then this deceleration would be consistent with a pure diffusion process, in which population growth is not involved. On the other hand, constant increase in radial spread of the population would be most consistent with the diffusion + exponential growth model.

Skellam (1951) made this comparison using data on a population starting with five muskrats (*Ondatra zebithica*) translocated into the countryside near Prague in 1905 (Fig. 7.7). Skellam’s analysis, supported by more rigorous analysis by Andow *et al.* (1990), clearly demonstrated that the radial spread of muskrats increased linearly over time, at a rate of 11 km/year (Fig. 7.8), thus supporting the exponential diffusion model.

Similar analysis of the naturally recovering population of California sea otters also supports the diffusion + exponential growth model (Lubina and Levin 1988), although the pattern is more complex. Radial spread to the north was slower than that to the southern California coast. Moreover, there seemed to be a dramatic jump in the distance dispersed per year as the otters moved into sandy coastal areas with less of their preferred rocky habitat.

Since those early days, there has been considerable development of alternative models of population spread. These recognize directional bias on the part of the

Fig. 7.7 Spatial spread over time of a small population of muskrats introduced into the countryside near Prague. (After Elton 1958.)

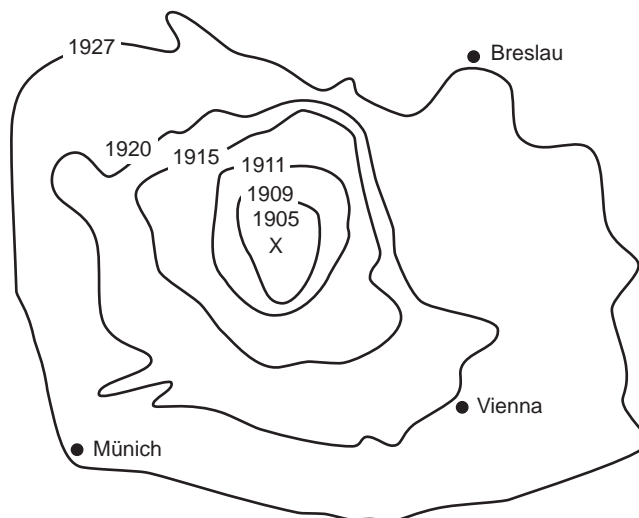
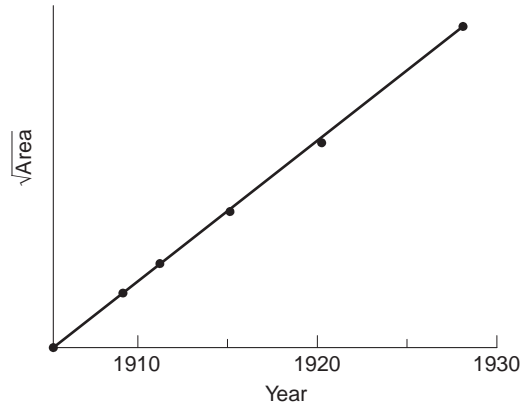


Fig. 7.8 Radial spread (measured as the square root of area) of the population of muskrats introduced into the countryside near Prague. (After Skellam 1951.)



disperser, changes in disperser motivation, or heterogeneous environmental effects on dispersal tendency (Turchin 1998). Nonetheless, the simple model of diffusive spread combined with exponential growth often does a tolerably good job of predicting patterns of population spread over time. These successful predictions suggest that both rapid population growth at the wave front and some degree of randomness in the pattern of movement contribute heavily to observed patterns of spread in many wildlife species. Both the theory and empirical mechanisms underlying animal movement across complex ecological landscapes are now developing rapidly, because both have important conservation implications.

7.7 Dispersal and the sustainability of metapopulations

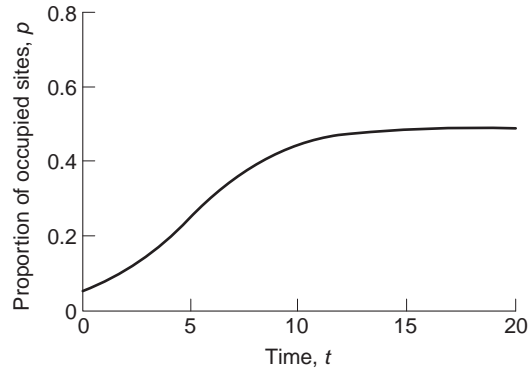
Dispersal also plays a key role in understanding the dynamics of species that are subdivided, for one reason or another, into discrete subpopulations. Provided that there is some degree of dispersal amongst subpopulations, ecologists refer to the larger aggregate as a **metapopulation**, or population of populations (Hanski and Gilpin 1997). Metapopulations can occur in a variety of contexts. Bird species on continental islands are an obvious example (Sæther *et al.* 1999). However, it is just as valid to think of butterflies inhabiting grassy glades in a matrix of boreal forest as a metapopulation (Hanski *et al.* 1994). Since 1980 there has been a surge in interest in metapopulation dynamics, fueled in part by the recognition that human environmental impacts often lead to fragmentation of natural areas, creating effective metapopulations from populations that were continuously distributed in the not-so-distant past. Here we outline some of the basic principles of metapopulation dynamics, particularly with relation to the impact of further habitat loss.

7.7.1 Metapopulation dynamics of a single species

There are many ways one can represent metapopulations, but the Levins model (Levins 1969) and its subsequent modifications (reviewed by Gyllenberg *et al.* 1997) have perhaps been the most influential. Let p be the proportion of occupied sites, c the probability of successful colonization, and e the probability of extinction of an occupied site. The rate of change in the number of occupied sites is calculated in the following manner:

$$\frac{dp}{dt} = cp(1 - p) - ep$$

Fig. 7.9 Dynamics over time of a metapopulation with colonization rate $c = 0.90$ and extinction rate $e = 0.45$.



The first term represents colonization of new sites, and the second term represents extinction. Provided that $c > e$, this model predicts that the proportion of occupied sites will converge over time on the following equilibrium:

$$p_{eq} = 1 - \frac{e}{c}$$

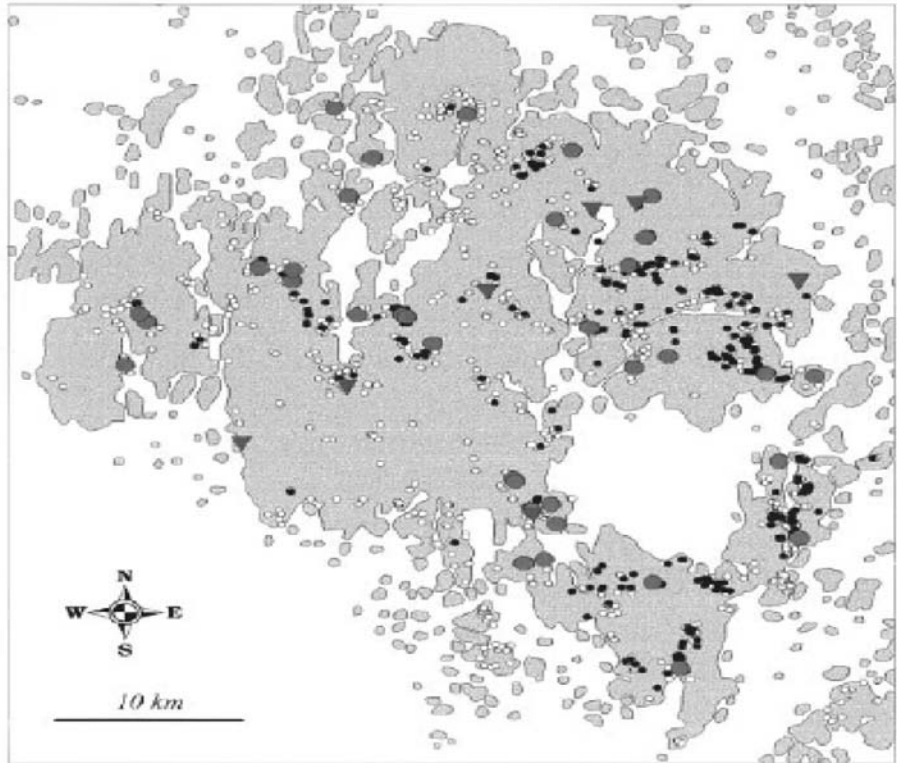
This can be clearly seen in the simulation shown in Fig. 7.9. The stability of the metapopulation at equilibrium belies a constant turnover of subpopulations. A substantial fraction of sites (45% in fact) go extinct per unit time. This extinction rate does not get translated into a dangerous collapse of population because of a stream of colonists from the remaining occupied sites. As we shall discuss in Chapter 17, local extinction is expected to become common when subpopulations have been reduced to low numbers, simply due to chance demographic events or rapid genetic loss. Hence, fragmentation of the environment into numerous small patches creates a situation in which local extinction risk is a very real possibility.

Empirical data consistent with the metapopulation scenario are accumulating. One of the best-documented examples is Hanski and co-workers' studies of the Glanville fritillary (*Melitaea cinxia*), an endangered butterfly inhabiting a number of forested islands in the eastern Baltic Sea, off the coast of Finland (Hanski *et al.* 1994; Saccheri *et al.* 1998). Field studies have concentrated on one island, Åland, in particular.

The spatial distribution of butterflies on Åland is quite patchy, in keeping with the patchy distribution of the larval food plants. The Finnish team repeatedly censused the number of butterfly larvae at each of several hundred locales. As the larvae are colonial and quite conspicuous, it is relatively straightforward to ascertain whether local extinction has taken place in the small grassy meadows. Results of the repeated censusing demonstrated that extinction was common amongst these local subpopulations, in accordance with metapopulation theory (Fig. 7.10).

As we might expect, many factors influenced the risk of extinction, including size of the local subpopulation, degree of genetic variability, and the degree of isolation from neighboring sites (Hanski *et al.* 1994; Saccheri *et al.* 1998). A high degree of turnover of local populations was normal, with the overall prevalence determined by the probabilities of colonization versus extinction. Unfortunately, recent population trends suggest that the Glanville fritillary may be fighting a losing battle against extinction.

Fig. 7.10 A map of Åland, showing sites of local subpopulations of the Glanville fritillary butterfly. Sites with suitable host plants occupied by larvae in 1995 are shown by filled symbols, whereas open circles depict unoccupied sites. A subset of 42 occupied sites were studied in detail, shown by large circles. Seven of these subpopulations, depicted by triangles, had gone extinct by the next sampling period. (After Saccheri *et al.* 1998.)



Well-studied examples of metapopulation dynamics in vertebrates are less common. Long-term studies of pool frogs along the coast of Sweden demonstrate a steady pattern of subpopulation turnover (Sjögren Gulve 1994). Similar patterns of extinction and recolonization have been shown in a number of other systems: cougars inhabiting chaparral shrub patches in urban southern California (Beier 1996), pikas living on mine tailings in the Sierra Nevada mountains of California (Smith and Gilpin 1997), sparrows on windswept islands off the coast of Norway (Sæther *et al.* 1999), and beavers inhabiting isolated ponds in Canada (Fryxell 2001). There is no doubt that the preconditions for metapopulation dynamics exist. The unresolved question is how common they might be.

7.7.2 Habitat loss and metapopulation collapse

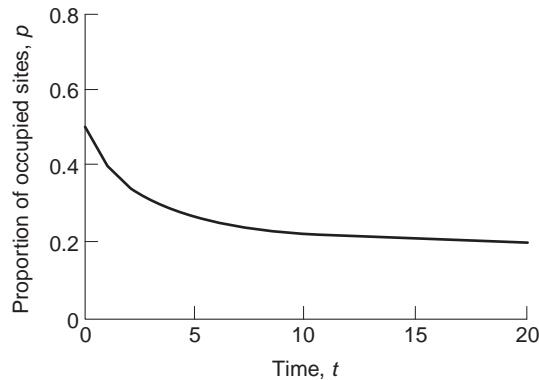
Levin's (1969) simple metapopulation model can be readily modified to predict the effect of habitat loss. Let H reflect the proportion of sites destroyed by man, so that any propagule that lands on a degraded site cannot persist. The dynamics of this degraded environment are depicted as follows:

$$\frac{dp}{dt} = cp(1 - H - p) - ep$$

As a result of habitat loss, the equilibrium level of occupancy is reduced (Fig. 7.11). If H is large enough, the metapopulation may not be able to persist at all. This is a simple, but graphic, way to look at the potential costs of habitat degradation. Empirical examples of habitat degradation leading to extinction are largely anecdotal, but nonetheless

Fig. 7.11

Metapopulation dynamics over time for the same parameters as in Fig. 7.9 ($c = 0.90$, $e = 0.45$), now with substantial habitat loss ($H = 0.3$) among the previously inhabitable sites. This leads to a reduction in the metapopulation equilibrium from 50% to 20%.



abound in the natural history literature, as we discuss in Chapter 18. The importance of habitat loss may be magnified in the future, if man does not learn to limit habitat fragmentation and prevent further alienation of subdivided patches of habitat.

7.7.3 Fragmented territorial systems

Through natural or human-influenced patterns of disturbance, suitable patches of habitat for breeding can become widely separated. Individuals setting up breeding territories must locate these suitable patches in an unfavorable matrix before they can set up a territory to attract mates (Lande 1987). Under many circumstances, the dynamics of territory occupancy by breeding pairs and their offspring are logically similar to those of a classic metapopulation (Noon and McKelvey 1996). Extinction is amplified when the probability of territory (patch) colonization is low relative to the probability of territory vacancy (local extinction) arising due to mortality. A key difference, however, is that successful breeding requires that both a male and a female independently discover a suitable territory site. At low probabilities of discovery, some individuals may never find mates. This **Allee effect** (after Allee (1938) who defined the process) could cause extinction if the overall level of territory occupancy falls below a critical level (Lande 1987, 1988; Courchamp *et al.* 2000a).

It is possible to imagine a metapopulation of local protected areas, each of whose internal dynamics are determined by the fragmented territory model (Lamberson *et al.* 1992, 1994). Under these circumstances, similar levels of species persistence could be obtained by a few large reserves, even if they are widely spaced, or a large number of small reserves, each of which is much more vulnerable in isolation to extinction. Depending on which circumstances prevail, the management priority would switch from maintaining territory quality within specific reserves to enhancing dispersal across a large network of reserves (Noon and McKelvey 1996).

A good example of this kind of situation involves the northern spotted owl (*Strix occidentalis*) of the western USA (Lande 1988). Spotted owls require substantial tracts of old growth forest for their breeding territories, but 80% or more of the mature forest in the northwestern USA has been logged over the past half century. As a consequence, local populations of owls are increasingly isolated from each other by large areas of clear-cutting. Moreover, variation in forest structure at the local level can influence territory occupancy. Concern about the long-term viability of northern spotted owl populations led to debates about appropriate management schemes for the public forest lands in the Pacific Northwest (Doak 1989; Lamberson *et al.* 1992, 1994; Doak and Mills 1994). The solution was both to control the future loss of mature forest and to manage the spatial pattern of forest utilization in such a way as to

maintain an effective metapopulation structure (Murphy and Noon 1992; Noon and McKelvey 1996). This kind of management controversy will only become more common with further fragmentation of existing wild lands.

7.7.4 Source–sink and island–mainland systems

Special kinds of metapopulation dynamics occur when some patches are large enough or productive enough to sustain permanent subpopulations, whereas other patches are small enough or unproductive enough that local extinction is common. If both the permanent patches and the transient patches can support positive population growth, such an arrangement is termed a **mainland–island system**. Examples include the checkerspot butterfly (*Euphydryas editha bayensis*), which inhabits scattered patches of serpentine soil in coastal California (Harrison *et al.* 1988) and spiders in the Bahama Islands (Schoener and Spiller 1987).

In other cases, only a fraction of patches can sustain positive subpopulation growth, whereas individuals in other patches always experience higher rates of mortality than birth. Such an arrangement is referred to as a **source–sink system**, with source sites supplying a steady stream of dispersers that fan out to surrounding sinks (Pulliam 1988; Pulliam and Danielson 1991). Despite the fact that sinks are incapable of supporting viable local populations, through immigration from source patches they can have substantial numbers of individuals. Beavers (*Castor canadensis*) inhabiting shallow lakes in the mixed deciduous and boreal forest of southern Ontario provide a good example of a mammalian species with source–sink dynamics (Fryxell 2001). Beavers at a small fraction of colonies have sufficient food supplies to support substantial production of offspring year after year. These populate the surrounding area when they disperse. Most of the other colonies rarely produce viable young.

Clearly, the conservation needs of mainland–island and source–sink systems differ from those of classic metapopulations. Mainland or source sites take on disproportionate importance in sustaining viable populations over the larger landscape. Loss of even small amounts of these critical source or mainland habitats could be unsustainable.

7.8 Summary

The distribution is the area occupied by a population or species, the dispersion is the pattern of spacing of the animals within it, and dispersal, migration, and local movement are the actions that modify dispersion and distribution. Dispersion and distribution are states; dispersal, migration, and local movement are processes. The edge of the distribution is that point at which, on average, an individual just fails to replace itself in the next generation. Its position may be set by climate, substrate, food supply, habitat, predators, or pathogens. The limiting factor can often be identified by the trend in density from the range boundary inward.

Dispersal plays a key role in dictating the rate of spread of a species reintroduced into a new area or one recovering from catastrophic decline. Diffusion models are often an effective means of modeling the spread of reintroduced species, particularly if they incorporate both demographic and random walk processes. We demonstrate the logical basis for the simplest random walk and diffusion models. Dispersal is also integral to the dynamics of organisms occupying spatially subdivided habitats forming metapopulations. Simple models demonstrate that the long-term persistence of metapopulations depends on the relative probabilities of extinction versus dispersive colonization. There is some empirical evidence for regular turnover of colonies and high rates of extinction and colonization. Variations on the metapopulation theme include source–sink systems, island–mainland systems, and metapopulations with internal territory structure.

8 Population regulation, fluctuation, and competition within species

8.1 Introduction

In this chapter we first describe the theory and evidence for the stability of populations through **regulation**. We then analyze the processes that can cause fluctuations and population cycles, using models to develop our understanding of the processes. Finally, we examine one of the major causes of regulation, namely competition between individuals for resources, or **intraspecific competition**. Other causes of regulation such as predation will be dealt with in Chapter 10. Chapter 12 outlines an alternative approach to analyzing resource use.

8.2 Stability of populations

If we look at long-term records of animal populations we see that some populations remain quite constant in size for long periods of time. Records of mute swans (*Cygnus olor*) in England from 1823 to 1872 (Fig. 8.1) illustrate that although the population fluctuates, it remains within certain limits (190–1150). Other populations, such as those of insects or house mice (*Mus domesticus*) in Australia (Fig. 8.2), fluctuate to a much greater extent and furnish no suggestion of an equilibrium population size. Nevertheless such populations do not always go extinct and they remain in the community for long periods. Occasionally one finds unusual situations where populations show regular cycles. The snowshoe hare (*Lepus americanus*) in northern

Fig. 8.1 Some populations remain within relatively close bounds over long time periods. The mute swan population of part of the river Thames, England (estimated by total counts) shows a steady level or gentle increase despite some perturbations due to severe winters, for example in 1946–47 and 1963–64. (Data from Cramp 1972.)

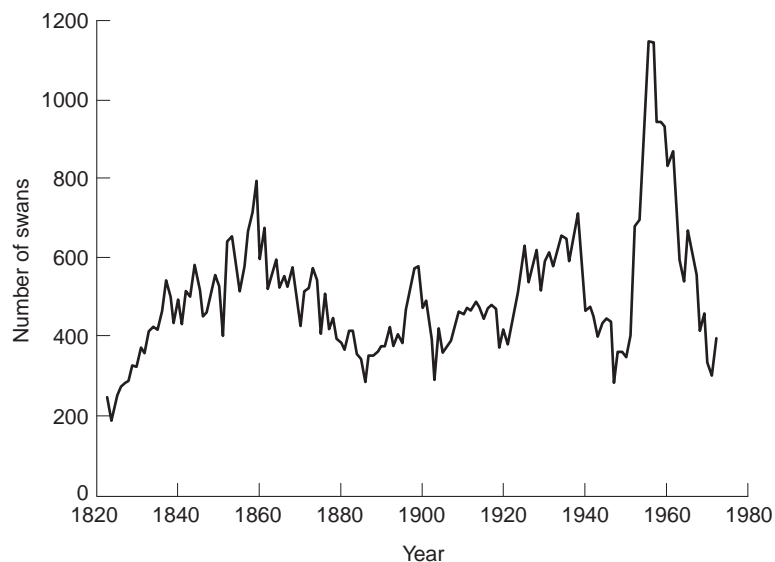


Fig. 8.2 Density indices for old female house mice on contour banks and in stubble fields of rice crops in southeastern Australia. Broken lines distinguish the crop cycle cohort of 1978–79 from that of 1977–78 and 1979–80. The extent of the peak in January 1980 is unknown due to a poisoning campaign. (After Redhead 1982.)

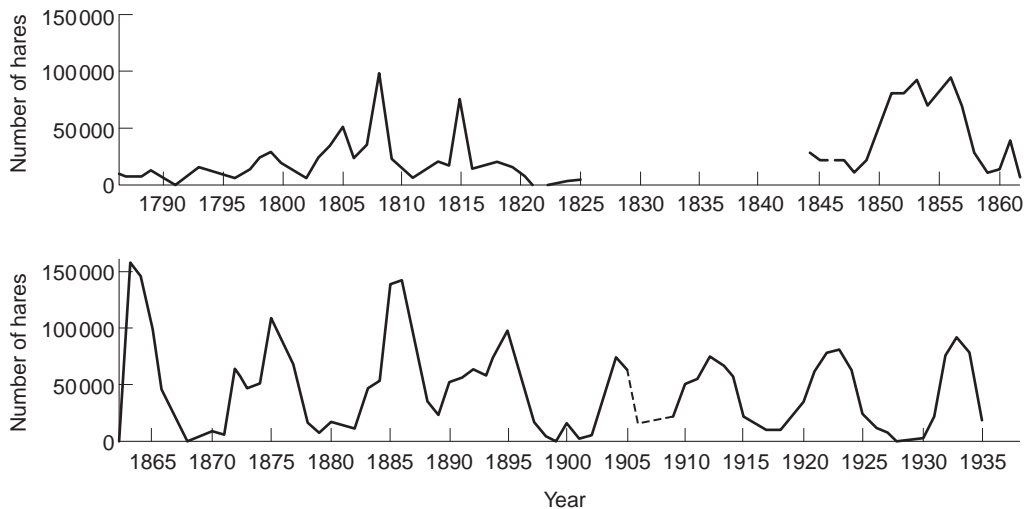
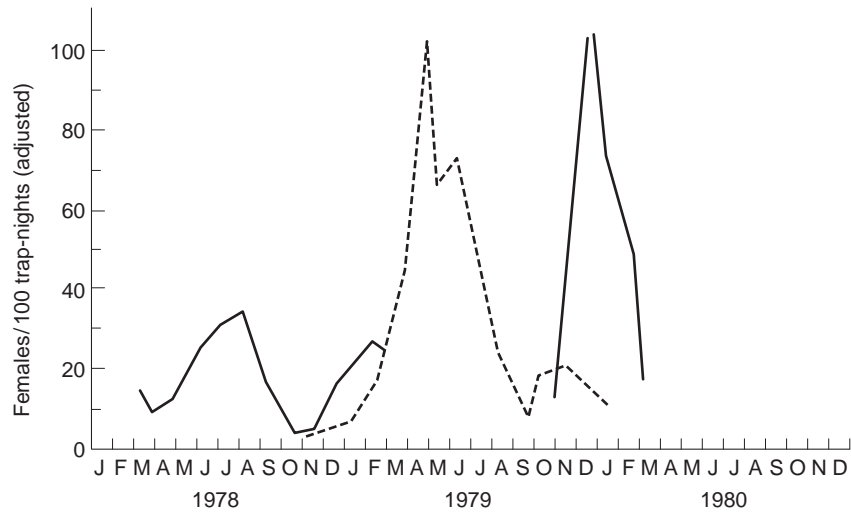


Fig. 8.3 Snowshoe hares in the boreal forest of Canada show regular fluctuations in numbers with a 10-year periodicity. Data are from the Hudson Bay Company fur records up to 1903 and questionnaires thereafter. (After MacLulich 1937.)

Canada shows the clearest (Fig. 8.3), as indicated by the furs collected by trappers for the Hudson Bay Company over the past two centuries (MacLulich 1937).

This relative constancy of population size, or at least fluctuation within limits, is in contrast to the intrinsic ability of populations to increase rapidly. The fact that population increase is limited suggests that there is a mechanism in the population that slows down the rate of increase and so regulates the population. We discuss first the theory for how populations might be **limited** and **regulated**.

8.3 The theory of population limitation and regulation

8.3.1 Density dependence

Populations have inputs of births and immigrants and outputs of deaths and emigrants. For simplicity we will confine discussion to a self-contained population having only births (B) and deaths (D) per unit time.

If either the proportion of the population dying increases or the proportion entering as births decreases as population density increases then we define these changes in proportions as being **density dependent**. The underlying causes for the changes in these rates are called **density-dependent factors**.

Births and deaths as a proportion of the population (B/N_t , D/N_t) can be related to the instantaneous birth (b) and death (d) rates in the following way.

The change in population per unit time is:

$$N_{t+1} - N_t = B - D$$

the instantaneous rate of increase (r) is given by:

$$r = b - d$$

and the finite rate of increase (λ) is given by:

$$\lambda = N_{t+1}/N_t = e^r$$

Therefore:

$$e^{b-d} = (N_{t+1}/N_t) = (B - D + N_t)/N_t$$

If $d = 0$, $D = 0$ then:

$$e^b = (B + N_t)/N_t = [1 + (B/N_t)]$$

and

$$b = \log_e [1 + (B/N_t)]$$

Similarly if $b = 0$, $B = 0$, and D/N_t is much less than 1, then:

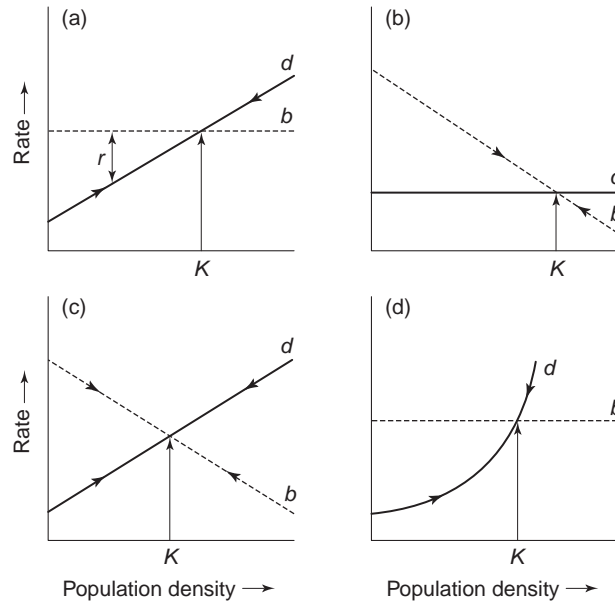
$$d = \log_e [1 + (D/N_t)]$$

If B and D fall in the range of 0–20% of the population then b and d are nearly linear on N , and they remain approximately linear even if B and D are 20–40% of N . This range covers most of the examples we see in nature, so for our purposes we can say that D/N_t and B/N_t change with density in the same way as do b and d , and both go through the origin.

In Fig. 8.4a we plot b against density (or population size) N as a constant so that it is a horizontal line. If we now plot d as an increasing function of density, we see that where the two lines cross, $b = d$, and the population is stationary, at the equilibrium point K . The difference between the b and d lines represents r , and this declines linearly as density increases, in the same way as it does for the logistic curve (see Section 8.6). In Fig. 8.4a the decline in r is due solely to d being density dependent.

Fig. 8.4 Model of density-dependent and density-independent processes.

(a) Birth rate, b , is held constant over all densities while mortality, d , is density dependent. The population returns to the equilibrium point, K , if disturbed. The instantaneous rate of increase, r , is the difference between b and d . (b) As in (a) but b is density dependent and d is density independent. (c) Both b and d are density dependent. (d) d is curvilinear so that the density dependence is stronger at higher population densities.



Since b (or B/N_t) is constant in this case we describe it as **density independent** (i.e. it is unrelated to density). In real populations density-independent factors such as weather may affect birth and death rates randomly. Rainfall acted in this way on greater kudu (*Tragelaphus strepsiceros*) in Kruger National Park, South Africa, causing mortality of juveniles (Owen-Smith 1990).

We can apply the same arguments if we assume that b is density dependent and d is density independent (Fig. 8.4b) or if both are density dependent (Fig. 8.4c). So far we have assumed that the density-dependent factor has a linear effect on rate of increase as in the logistic curve. However, density-dependent mortality is more likely to be curvilinear, as in Fig. 8.4d.

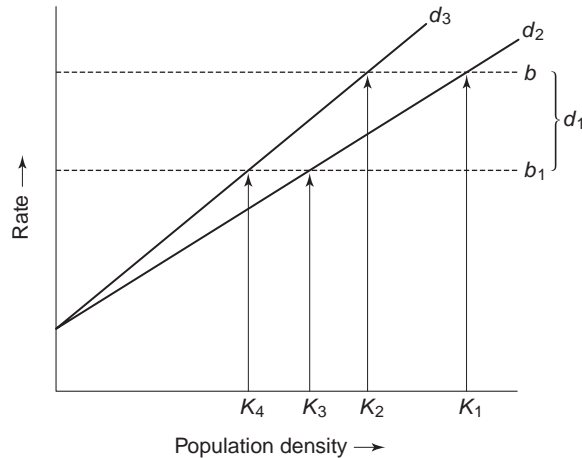
8.3.2 Limitation and limiting factors

In Fig. 8.5 we take the argument a little further. Let us assume a constant (density-independent) birth rate b . Shortly after birth a density-independent mortality d_1 (depicted here as a constant) kills some of the babies so that inputs are reduced to b_1 . There follows a density-dependent mortality d_2 , and the population reaches an equilibrium at K_3 . If mortality d_1 had not occurred (or was smaller), the equilibrium population would be at K_1 . Therefore, the presence or absence of the density-independent factor causing d_1 alters the size of the equilibrium population.

The strength or severity of the density-dependent factor is indicated by the slope of d_2 . If the density-dependent factor becomes stronger such as to produce d_3 instead of d_2 , the slope becomes steeper and the equilibrium population drops from K_3 to K_4 (or K_1 to K_2 if d_1 is absent). Thus, altering the strength of density-dependent factors also alters the size of the equilibrium population.

We define the process determining the size of the equilibrium population as **limitation**, and the factors producing this are **limiting factors**. We can see, therefore, that both density-dependent and density-independent factors affect the equilibrium population size and so they are all limiting factors. Any factor that causes mortality or affects birth rates is a limiting factor.

Fig. 8.5 Model showing that the equilibrium point, K , can vary with both density-dependent and density-independent processes. Birth rate, b , is held constant over all densities. In sequence, a density-independent mortality d_1 reduces the input to the population to b_1 . There follows a density-dependent mortality d_2 or d_3 . The intercept of b or b_1 with d_2 or d_3 determines the equilibrium (K_1 – K_4).



8.3.3 Regulation

Populations are often disturbed from their equilibrium, K , by temporary changes in limiting factors (a severe winter or drought or influx of predators might reduce the population; a mild winter or good rains might increase it). The subsequent tendency to return to K is largely due to the effect of density-dependent factors, and this process is called **regulation**. Therefore, regulation is the process whereby a density-dependent factor tends to return a population to its equilibrium. We say “tends to return” because the population may be continually disturbed so that it rarely reaches the equilibrium. Nevertheless this tendency to return to equilibrium results in the population remaining within a certain range of population sizes. Superficially it appears as if the population has a boundary to its size, and it fluctuates randomly within this boundary. However, it is more constructive to picture random fluctuations in both the density-independent (d_1) and density-dependent (d_2) mortalities as the shaded range in Fig. 8.6a. This results in a fluctuation of the equilibrium population

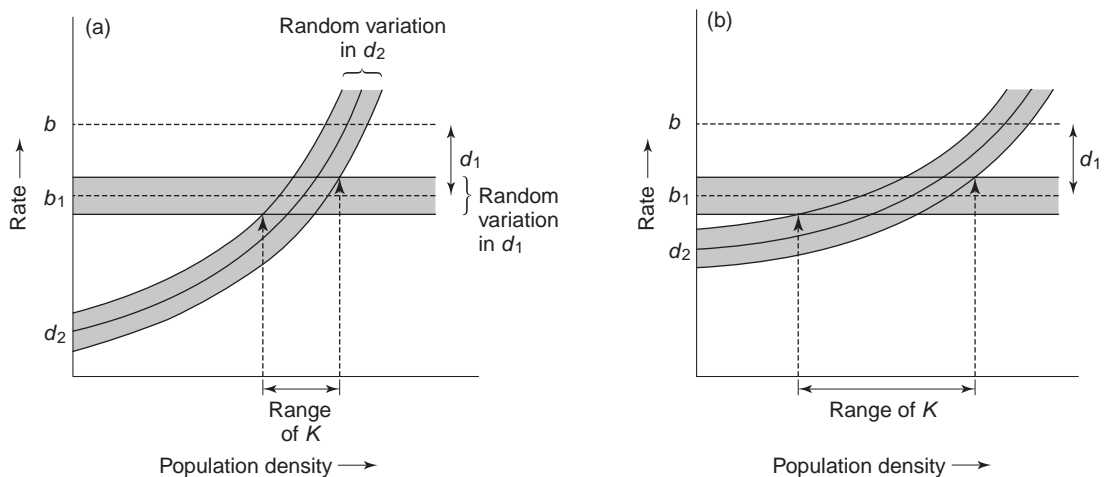


Fig. 8.6 Random variation in the mortalities d_1 and d_2 (indicated by the shaded area) are the same in (a) and (b). In (a) there is stronger density dependence at the intercept of b_1 and d_2 than in (b), and this difference results in a smaller range of equilibria, K , in (a) than in (b).

indicated by the range of K . Figure 8.6a shows that this range of K is relatively small when the density-dependent mortality is strong (steep part of the curve). Figure 8.6b shows the range of K when the density-dependent mortality is weak. We can see that the range of K (which we see in nature as fluctuations in numbers) is very much greater when the density-dependent mortality is weak than when it is strong. Note in Figs 8.6a and 8.6b that differences in amplitude of fluctuations are due to changes in the strength of the density-dependent mortality because we have held density-independent (random) mortality constant in this case.

8.3.4 *Delayed and inverse density dependence*

Some mortality factors do not respond immediately to a change in density but act after a delay. Such **delayed density-dependent factors** can be predators whose populations lag behind those of their prey, and food supply where the lag is caused by the delayed action of starvation. Both causes can have a density-dependent effect on the population but the effect is related to density at some previous time period rather than the current one. For example, a 34-year study of white-tailed deer in Canada indicated that both the population rate of change and the rate of growth of juvenile animals are dependent on population size several years previously, rather than current population size (Fryxell *et al.* 1991). A similar relationship was found with winter mortality of red grouse (*Lagopus lagopus*) in Scotland (Fig. 8.11). Delayed density dependence is indicated when mortality is plotted against current density and the points show an anticlockwise spiral if they are joined in temporal sequence (Fig. 8.11). These delayed mortalities usually cause fluctuations in population size, as we will demonstrate later in this chapter.

Predators can also have the opposite effect to density dependence, called an **inverse density-dependent** or **depensatory** effect. In this case predators have a destabilizing effect because they take a decreasing proportion of the prey population as it increases, thus allowing the prey to increase faster as it becomes larger. Conversely, if a prey population is declining for some reason, predators would take an increasing proportion and so drive the prey population down even faster towards extinction. In either case we do not see a predator–prey equilibrium. We explore this further in Chapter 10.

8.3.5 *Carrying capacity*

The term **carrying capacity** is one of the most common phrases in wildlife management. It does, however, cover a variety of meanings and unless we are careful and define the term, we may merely cause confusion (Caughley 1976, 1981). Some of the more common uses of the term are discussed below.

Ecological carrying capacity

This can be thought of abstractly as the K of the logistic equation, which we derive later in this chapter (Section 8.6). In reality it is the natural limit of a population set by resources in a particular environment. It is one of the equilibrium points that a population tends towards through density-dependent effects from lack of food, space (e.g. territoriality), cover, or other resources. As we discussed earlier, if the environment changes briefly it deflects the population from achieving its equilibrium and so produces random fluctuations about that equilibrium. A long-term environmental change can affect resources, which in turn alters K . Again the population changes by following or tracking the environmental trend.

There are other possible equilibria that a population might experience through regulation by predators, parasites, or disease. Superficially they appear similar to that equilibrium produced through lack of resources because if the population is disturbed

through culling or weather events it may return to the same population size. To distinguish the equilibria produced by predation, by resource limitation, and by a combination of the two, we need to know whether predators or resources or both are affecting b and d .

Economic carrying capacity

This is the population level that produces the maximum offtake (or maximum sustained yield) for culling or cropping purposes. It is this meaning that is implied when animal production scientists and range managers refer to livestock carrying capacity. We should note that this population level is well below the ecological carrying capacity. For a population growing logistically its level is $1/2K$ (Caughley 1976).

Other senses of carrying capacity

We can define carrying capacity according to our particular land use requirements. At one extreme we can rate the carrying capacity for lions on a Kenya farm or wolves on a Wyoming ranch as zero (i.e. farmers cannot tolerate large predators killing their livestock).

A less extreme example is seen where the aesthetic requirements of tourism require reducing the impact of animals on the vegetation. Large umbrella-shaped *Acacia tortilis* trees make a picturesque backdrop to the tourist hotels in the Serengeti National Park, Tanzania. In the early 1970s, elephants began to knock over these trees. Whereas elephants could be tolerated at ecological carrying capacity in the rest of the park, in the immediate vicinity of the hotels the carrying capacity for elephants was much lower and determined by human requirements for scenery.

8.3.6 Measurements of birth and death rates

Birth rates are inputs to the population. Ideally we would like to measure conception rates (**fecundity**), pregnancy rates in mammals (**fertility**), and births or egg production. In some cases it is possible to take these measurements, as in the Soay sheep of Hirta (Clutton-Brock *et al.* 1991). Pregnancies can be monitored by a variety of methods including ultrasound, X-rays, blood protein levels, urine hormone levels, and rectal palpation of the uterus (in large ungulates). In many cases, however, these are not practical for large samples from wild populations.

Births can be measured reasonably accurately for seal species where the babies remain on the breeding grounds throughout the birth season. Egg production, egg hatching success, and fledgling success can also be measured accurately in many bird populations. However, in the majority of mammal species birth rates cannot be measured accurately, either because newborn animals are rarely seen (as in many rodents, rabbits, and carnivores) or because many newborn animals die shortly after birth and are not recorded in censuses (as in most ungulates). In these cases we are obliged to use an approximation to the real birth rate, such as the proportion of the population consisting of juveniles first entering live traps for rodents and rabbits, or juveniles entering their first winter for carnivores and ungulates. These are valid measures of recruitment.

Death rates are losses to the population. Ideally they should be measured at different stages of the life cycle to produce a life table (see Section 6.4). Once sexual maturity is reached, age classes often cannot be identified and all mortality after that age is therefore lumped as “adult” mortality. Mortality can be measured directly by using mortality radios which indicate when an animal has died, as was done by Boutin *et al.* (1986) and Trostel *et al.* (1987) for snowshoe hares in northern Canada.

Survivorship can be calculated over varying time periods by the method of Pollock *et al.* (1989).

Mortality caused by predators can also be measured directly if the number of predators (numerical response) and the amount eaten per predator (functional response) are known (see also Chapters 5, 10, and 12). Such measurements are possible for those birds of prey that regurgitate each day a single pellet containing the bones of their prey. With appropriate sampling, the number of pellets indicates the number of predators, and prey per pellet shows the amount they eat. This method was used for raptors (in particular the black-shouldered kite, *Elanus notatus*) eating house mice during mouse outbreaks in Australia (Sinclair *et al.* 1990).

8.3.7 Implications

We should be aware of a number of problems associated with the subject of population limitation and regulation:

- 1 Much of the literature uses the terms limitation and regulation in different ways. In many cases the terms are used synonymously, but the meanings differ between authors. Since any factor, whether density dependent or density independent, can determine the equilibrium point for a population, any factor affecting b or d is a limiting factor. It is, therefore, a trivial question to ask whether a certain cause of mortality limits a population – it has to. The more profound question is in what way do mortality or fecundity factors affect the equilibrium.
- 2 Regulation requires, by our definition, the action of density-dependent factors. Density dependence is necessary for regulation but may not be sufficient. First, the particular density-dependent factor that we have measured, such as predation, may be too weak, and other regulating factors may be operating. Second, some density-dependent factors have too strong an effect, and consequently cause fluctuations rather than a tendency towards equilibrium (see Section 8.7).
- 3 The demonstration of density dependence at some stage in the life cycle does not indicate the cause of the regulation. For example, if we find that a deer population is regulated through density-dependent juvenile mortality, we do not have any indication from this information alone as to the cause of the mortality. Correlation with population size is merely a convenient abbreviation that hides underlying causes. Density itself is not causing the regulation; the possible underlying factors related to density are competition for resources, competition for space through territoriality, or an effect of predators, parasites, and diseases (see Section 8.7).

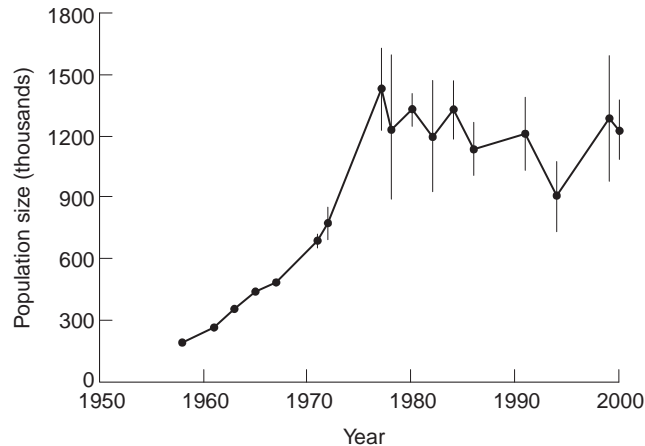
8.4 Evidence for regulation

There are three ways of detecting whether populations are regulated. First, as we have seen in Section 8.3.3, regulation causes a population to return to its equilibrium after a perturbation. Perturbation experiments should therefore detect the return towards equilibrium. Similarly, natural variation in population density, provided it is of sufficient magnitude, can be used to test whether per capita growth rates decline with density (Chapter 15). Second, if we plot separate and independent populations at their natural carrying capacity against some index of resource (often a weather factor) there should be a relationship. Third, we can try to detect density dependence in the life cycle.

8.4.1 Perturbation experiments

If a population is moved experimentally either to below or above its original density and then returns to this same level we can conclude that regulation is occurring. An example of downward perturbation is provided by the northern elk herd of

Fig. 8.7 The wildebeest population in Serengeti increased to a new level determined by intraspecific competition for food, after the disease rinderpest was removed in 1963. (After Mduma *et al.* 1999 and unpublished data.)



Yellowstone National Park (Houston 1982). Before 1930, the population estimates ranged between 15,000 and 25,000. Between 1933 and 1968 culling reduced the population to 4000 animals. Culling then ceased and the population rebounded to around 20,000 (Coughenour and Singer 1996). This result is consistent with regulation through intraspecific competition for winter food (Houston 1982), since there were no natural predators of elk in Yellowstone until the return of wolves in the early 1990s.

Density is usually recorded as numbers per unit area. If space is the limiting resource (as it might be in territorial animals), or if space is a good indicator of some other resource such as food supply, numbers per unit area will suffice in an investigation of regulation. However, space may not be a suitable measure if density-independent environment effects (e.g. temperature, rainfall) cause fluctuations in food supply. It may be better to record density as animals per unit of available food or per unit of some other resource.

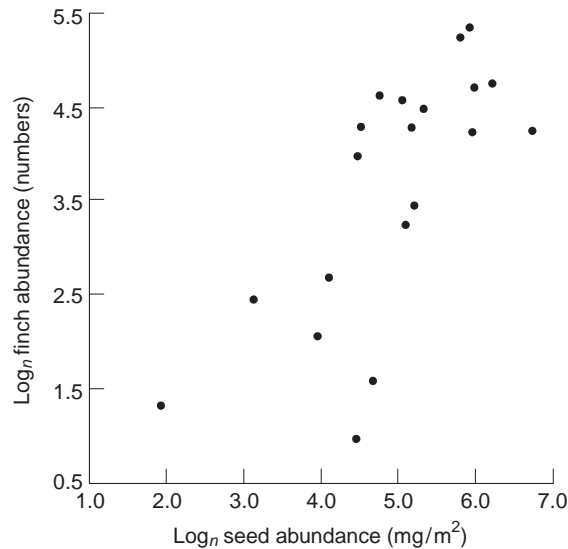
The Serengeti migratory wildebeest experienced a perturbation (Fig. 8.7) when an exotic virus, rinderpest, was removed. The population increased fivefold from 250,000 in 1963 to 1.3 million in 1977 and then leveled out (Mduma *et al.* 1999). This example is less persuasive than that of the Yellowstone elk because the pre-rinderpest density (before 1890) was unknown, but evidence on reproduction and body condition suggests that rinderpest held the population below the level allowed by food supply, a necessary condition for a perturbation experiment implicating a disease.

A case of a population perturbed above equilibrium is provided by elephants in Tsavo National Park, Kenya (Laws 1969; Corfield 1973). From 1949 until 1970, the population had been increasing due in part to immigration from surrounding areas where human cultivation had displaced the animals. A consequence of this artificial increase in density was depletion of the food supply within reach of water. In 1971, the food supply ran out and there was starvation of females and young around the water holes. After this readjustment of density, the vegetation regenerated and starvation mortality ceased.

8.4.2 Mean density and environmental factors

A population uninfluenced by dispersal and unregulated (i.e. it has no density-dependent factors affecting it) will fluctuate randomly under the influence of weather and will eventually drift to extinction (DeAngelis and Waterhouse 1987).

Fig. 8.8 The total abundance of seed-eating finches in savanna habitats of Kenya is related to the abundance of the food supply. Such a positive relationship in unconnected populations may demonstrate regulation. (After Schluter 1988.)



Just by chance there may be for a time a correlation between density and environmental factors. However, if we take many separate populations, the probability that all of them are simultaneously correlated with an environmental factor by chance alone is very small. Therefore, if we find a correlation between mean densities from independent populations with an environmental factor, there is a strong inference that weather is influencing some resource for which animals are competing, and which results in regulation about some equilibrium point.

An example of this approach is shown in Schluter's (1988) study of seed-eating finches in Kenya (Fig. 8.8): finch abundance from various populations is correlated with seed abundance. Other examples of density correlated with weather factors are given in Sinclair (1989).

8.4.3 Examples of density dependence

As we discussed in Section 8.3.7, density dependence is a necessary but not sufficient requirement to demonstrate regulation. There are an increasing number of studies in the bird and mammal literature demonstrating density-dependent stages in the life cycle. For birds (Fig. 8.9a), the long-term study on great tits (*Parus major*) at Oxford, England has shown that winter mortality of juveniles was related to the number of juveniles entering the winter (McCleery and Perrins 1985). In contrast (Fig. 8.9b), it was early chick mortality in summer that was density dependent for the English partridge (*Perdix perdix*) (Blank *et al.* 1967).

For mammals, density-dependent juvenile mortality has been recorded for red deer on the island of Rhum, Scotland (Clutton-Brock *et al.* 1985) (Fig. 8.10a), for reindeer in Norway (Skogland 1985) (Fig. 8.10b), for feral donkeys (*Equus asinus*) in Australia (Choquenot 1991), and for greater kudu in South Africa (Owen-Smith 1990). Adult mortality was density dependent for African buffalo in Serengeti (Sinclair 1977). In each case, the cause was lack of food at critical times of year. Reproduction is known to be density dependent in both birds (Arcese *et al.* 1992) and mammals (Clutton-Brock *et al.* 1991). Figure 8.10c shows that the proportion of Soay sheep that give birth at 12 months of age declines with density. Fowler (1987) reports over

Fig. 8.9 Examples of density-dependent mortality in birds. (a) Great tit (*Parus major*) overwinter mortality (log of [juveniles in winter/first year breeding population]) plotted against log juvenile density in winter. (After McCleery and Perrins 1985.) (b) Chick mortality of European partridge (*Perdix perdix*) (measured as log hatching population/log population at 6 weeks) plotted against log hatching population, in Hampshire, England. (After Blank *et al.* 1967.)

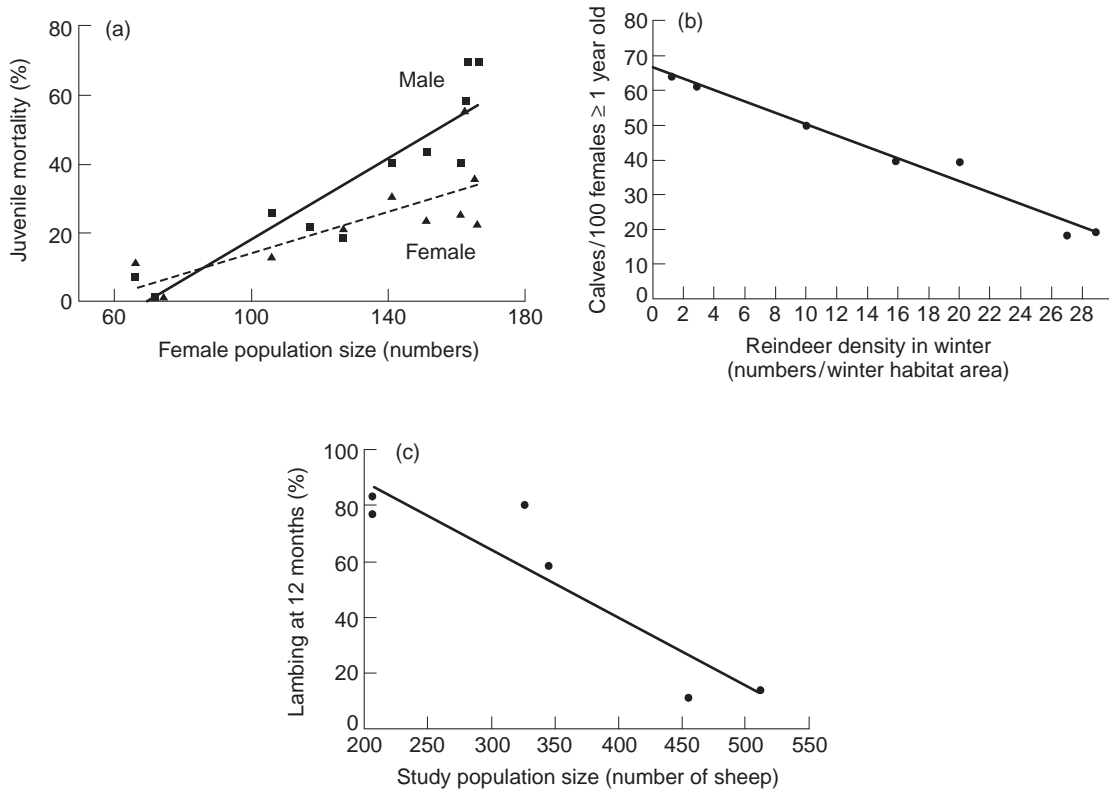
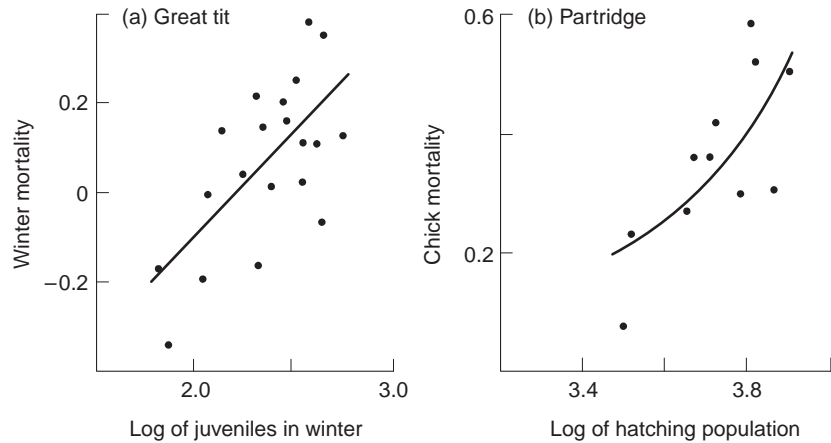
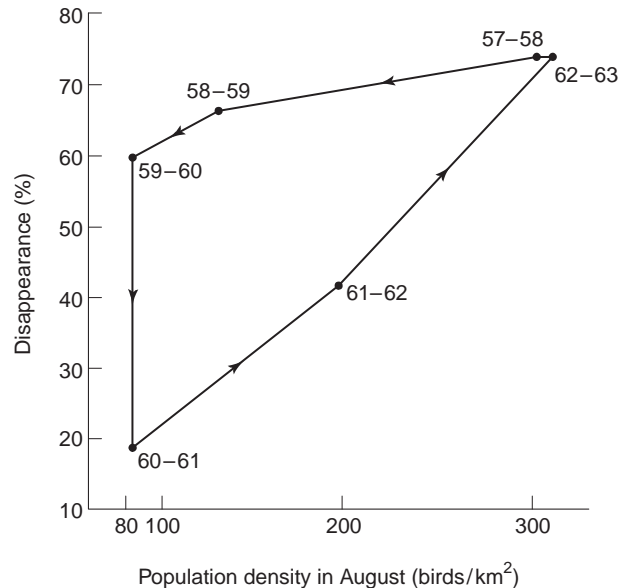


Fig. 8.10 Density dependence in large mammals. (a) Juvenile mortality of male and female red deer on the island of Rhum, Scotland. (After Clutton-Brock *et al.* 1985.) (b) Juvenile recruitment per 100 female reindeer older than 1 year in Norway. (After Skogland 1985.) (c) The fertility rate of 1-year-old Soay sheep on St Kilda island. (After Clutton-Brock *et al.* 1991.)

Fig. 8.11 The proportion of a red grouse population in Scotland which disappears over winter (August–April) is related to population density in the previous August in a complex way. Mortality varied according to whether the population was increasing or decreasing. By joining the points sequentially an anticlockwise cycle is produced, indicating a delayed density-dependent effect in the cause of the mortality. By plotting the percentage disappearance against density 1 year earlier, a closer fit can be obtained for a regression line. Thus the delay is 1 year. Numbers at the points are years. (After Watson and Moss 1971.)



100 studies of terrestrial and marine mammal populations where density dependence was detected.

Delayed density dependence has been recorded in winter mortality of snowshoe hares in the Yukon and in overwinter mortality of red grouse in Scotland (Watson and Moss 1971) (Fig. 8.11). For the hares the delay appears to have been due to a lag of 1–2 years in the response of predator populations to changing hare numbers (Trostel *et al.* 1987), while for the grouse the delay came from density responding to food conditions in the previous year (see Section 8.8.3).

8.5 Applications of regulation

Causes of population change can be divided into (i) those that disrupt the population and often result in “outbreaks,” and which can be either density dependent or density independent; and (ii) those that regulate and therefore return the population to original density after a disturbance (Leirs *et al.* 1997). These are always density dependent.

Knowledge of regulation may be useful for management of house mice (*Mus domesticus*) plagues in Australia. In one experimental study (Barker *et al.* 1991), mice in open-air enclosures were contained by special mouse-proof fences. The objective was to create high densities, thus mimicking plague populations, in order to test the regulatory effect of a nematode parasite (*Capillaria hepatica*). It turned out that they could not test the effect of the parasite because other factors regulated the population and thus obscured any parasite effect. The replicated populations declined simultaneously. Why did this happen? By dividing up the life cycle into stages they found that late juvenile and adult mortality was strongly density dependent but that other stages, including fertility and newborn mortality, were not. This allowed them to discount causes that would affect reproduction and focus more closely on what was happening amongst adults, in particular the social interactions of mice.

Other studies suggest that mouse populations in Australia may be regulated by predators, disease, and juvenile dispersal (Redhead 1982; Sinclair *et al.* 1990). Under

conditions of superabundant food following good rains, the reproductive rate of females increased faster than the predation rate, and an outbreak of mice occurred. The implication of these results for management is that if reproduction could be reduced, for example through infections of the *Capillaria* parasite, then predation may be able to prevent outbreaks even in the presence of abundant food for the mice.

8.6 Logistic model of population regulation

In Chapter 6, we derived geometric and exponential growth models. In 1838, Pierre-Francois Verhulst published a paper (Verhulst 1838) that challenged the assumption of unlimited growth implicit in these models. Verhulst argued that the per capita rate of change (dN/Ndt) should decline proportionately with population density, simply due to a finite supply of resources being shared equally among individuals. If each individual in the population gets a smaller slice of the energy “pie” as N increases, then this would prevent them from devoting as much energy to growth, reproduction, and survival than would be possible under ideal conditions. As we saw in Chapter 6, changes in demographic parameters lead to corresponding changes in the finite rate of population growth λ_t or its equivalent exponential rate r_t , where t denotes a specific point in time. Other factors, such as risk of disease, shortage of denning sites, or aggressive interactions among population members, might also cause the rate of population growth to decline with population size. The simplest mathematical depictions of such phenomena are commonly termed “logistic” models.

There are numerous ways to represent logistic growth. For simplicity, we will focus on population growth modeled in discrete time, which is often a reasonable approximation for species that live in a seasonal environment. One of the most commonly used forms is called the Ricker equation, in honor of the Canadian fisheries biologist, Bill Ricker, who first suggested its application to salmon stocks (Ricker 1954):

$$N_{t+1} = N_t e^{r_{\max} \left(1 - \frac{N_t}{K}\right)}$$

The Ricker logistic equation represents the exponential rate of increase under ideal conditions as r_{\max} , with a proportionately slower rate of increase with each additional individual added to the population. When the rate of increase has slowed to the point that births equal deaths, then the population has reached its carrying capacity K . These two population parameters (r_{\max} and K) dictate how fast the population recovers from any perturbation to abundance.

A population growing according to the logistic equation would have slow growth when N is small, grow most rapidly when N is of intermediate abundance, and grow slowly again as N approaches carrying capacity K (Fig. 8.12). This kind of sigmoid or S-shaped pattern is often termed **logistic growth**.

At first, it may seem somewhat counterintuitive that a proportional decline in per capita demographic rates could produce the non-linear growth pattern seen in Fig. 8.12. The answer lies in the fact that population changes are dependent on both population size and the per capita growth rate, in much the same way that growth of a bank account depends both on the money already in the account and the interest rate. When a population is small, the per capita rate of change will tend to be large, in fact close to r_{\max} , because either birth rates are high or mortality rates are low. Nonetheless, the population will still display a slight change from one year to the next because the population is small. At the other end of the spectrum, despite

Fig. 8.12 Population growth according to the logistic equation, with $r_{\max} = 0.5$, initial population density $N_0 = 1.5$, and carrying capacity $K = 100$.

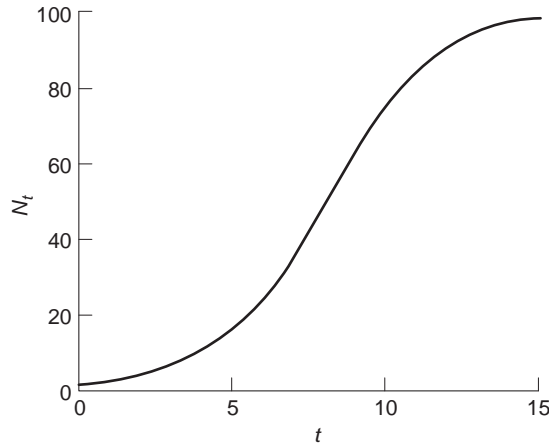
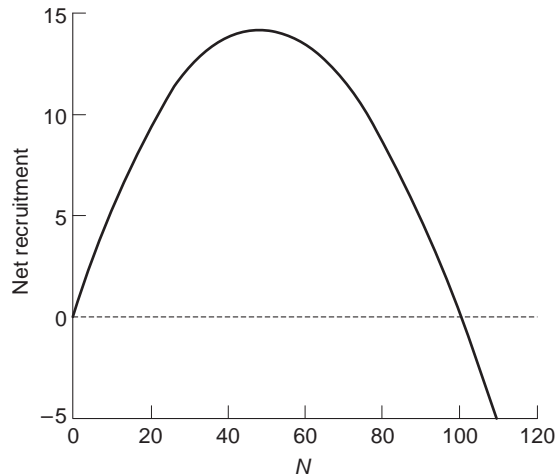


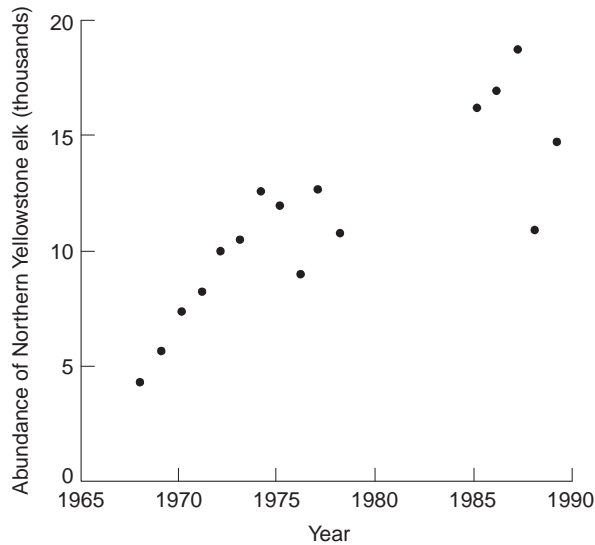
Fig. 8.13 Net recruitment ($N_{t+1} - N_t$) as a function of population density N_t , according to the Ricker logistic growth model, with $r_{\max} = 0.5$ and $K = 100$.



the fact that N is enormous, the population will similarly display modest change from year to year. This is because the per capita rate of growth is small, because either birth rates are low or mortality rates are high. It is only when the population is of intermediate size and growing at an intermediate per capita rate that growth is maximized (Fig. 8.13).

Population data displaying the classic sigmoid pattern of change are rare. It will only be seen when a population is reduced to very low initial density and then monitored closely over an extended period. So, logistic growth will not be obvious in most populations that we might see around us in nature, which are presumably close to their carrying capacity. In some cases, however, populations have been perturbed (reduced) to low densities, and give us a rare glimpse of logistic growth in the field. For example, as we discussed earlier, the Yellowstone elk herd has been aggressively culled at various times in the past, particularly in the late 1960s. Cessation of culling operations, stimulated by a new policy of natural regulation in US National Parks, led to a subsequent pattern of elk recovery reminiscent of the sigmoid pattern predicted by the logistic model (Fig. 8.14). Similarly, release of the Serengeti wildebeest population from the exotic disease rinderpest led to a subsequent sigmoid pattern

Fig. 8.14 Population dynamics of Northern Yellowstone elk between 1968 and 1989. (Data from Coughenour and Singer 1996.)



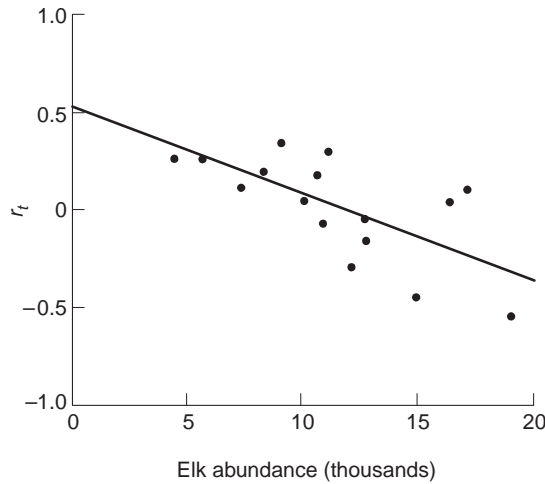
of change (Fig. 8.7) reminiscent of the logistic model. Indeed, perturbation is an important ingredient in detecting natural regulation and logistic growth, because it gives us evidence to work with, unlike populations kept close to their ecological carrying capacity. We demonstrate how to estimate the parameters for the Ricker logistic model, and compare it with other possible population growth models, in Chapter 15.

All environments show some degree of variability in conditions from year to year. Such stochastic or random variation can have a strong influence on the dynamics of even tightly regulated species. We can explore this by applying the Ricker logistic model to some typical empirical data. Figure 8.14 shows records of elk censused in Northern Yellowstone National Park between 1968 and 1989 (Coughenour and Singer 1996). We see that there is the barest hint of a sigmoid pattern in these data. Nonetheless, exponential growth rates r_t calculated over this two-decade period show a strong density-dependent decline in growth rates when the population is large (Fig. 8.15).

The scatter around the regression line (termed “residual” variation) in Fig. 8.15 shows that natural regulation explains only part of the demographic response by a wild population to changes in density. Even when the population is tightly regulated, as is obviously the case here, there can be considerable variation in growth rates from year to year that is not explained by density dependence. Some of this variability is due to stochastic climatic variation that characterizes every natural environment, some places more than others. In the case of Northern Yellowstone elk, for example, precipitation in the preceding 2 years is probably responsible for much of the residual variation shown in Fig. 8.15, judging from its effect on offspring production and survival rates (Coughenour and Singer 1996). This probably stems from a strong linkage between precipitation and forage availability to elk.

Variability in population growth rates can also stem from “demographic stochasticity.” This term refers to variation in the numbers of individuals born or dying per unit time, simply due to chance (Chapter 17). The principle is familiar to anyone who has played a game of cards or spun a roulette wheel. For a given probability of survival, say 0.25, we do not necessarily expect exactly a quarter of the population

Fig. 8.15 Exponential growth rates for Northern Yellowstone elk between 1968 and 1989 in relation to population density at the beginning of each yearly interval. (Data from Coughenour and Singer 1996.)



to survive, but rather anticipate that by chance sometimes a larger fraction will survive, sometimes a smaller fraction. We consider this process in more exact mathematical detail in Chapter 17, when we discuss population viability analysis. In wildlife management we need to disentangle demographic from environmental sources of stochasticity (Sæther *et al.* 2000; Bjørnstad and Grenfell 2001).

We should include in our population models the variability in growth rates due to environmental and demographic stochasticity. We do this by simulating natural stochastic variation and adding this variation to the exponential growth rate r_t predicted by population density. We first need to calculate the residual variation in growth from the data in Fig. 8.15:

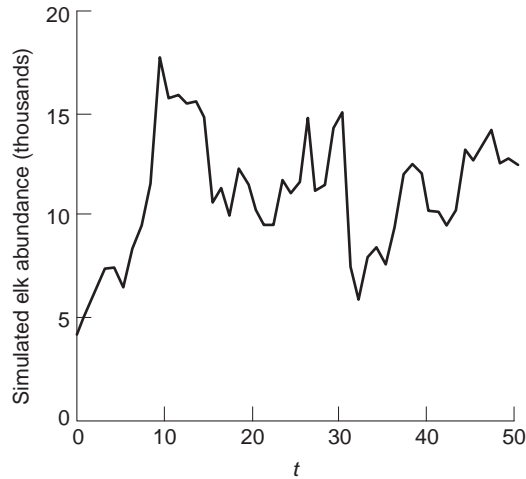
$$\sigma = \sqrt{\frac{\sum_{t=0}^{15} [r_t - (0.518 - 0.00004404N_t)]^2}{16}}$$

where 0.518 is the intercept (r_{\max}) of the regression line drawn through the observed values of r_t versus N_t , and -0.00004404 is the slope. We calculate the deviation between each observation of r and the value predicted by the regression line at that population density, square each deviation to standardize positive versus negative values, sum the squared deviations, and divide by the sample size (16 in this case) to estimate the mean-squared deviation. This is the residual variability, denoted by σ^2 . For the Northern Yellowstone elk, $\sigma^2 = 0.0361$.

Once equipped with an estimate of the residual variation based on the observed data, we draw values of the random variable ε from a bell-shaped (i.e. normal) probability distribution with the same magnitude of residual variation σ . In MATHCAD, this normal probability distribution is the function called **rnorm**, which also requires the user to input the required number of random values, and mean and standard deviation of the normal distribution from which these values will be drawn. For the elk example:

$$\varepsilon = \text{rnorm}(51, \mu, \sigma)$$

Fig. 8.16 Simulated dynamics of elk, based on the Yellowstone National Park population. (Data from Coughenour and Singer 1996.)



where $\mu = 0$ and $\sigma = 0.19$. We then combine the random normal deviate at any point in time (ε_t) with the rate of increase predicted by the Ricker logistic equation, $r_{\max}(1 - N_t/K)$, to predict changes in abundance. We use a different symbol (n_t) for the simulated density:

$$n_{t+1} = n_t e^{r_{\max} \left(1 - \frac{n_t}{K}\right) + \varepsilon_t}$$

We plot the simulated elk data (n_t) in Fig. 8.16. We see that the trends in the simulated population are completely different from those of the real population (Fig. 8.14), but the overall magnitude of variability is similar. This similarity occurs because we have included both the stochastic (environmental and demographic) processes that tend to perturb the population away from its carrying capacity and the natural regulatory processes that tend to restore the population, once perturbed. Both processes are common in the natural world, and therefore we need to accommodate them in our management planning.

Such stochastic simulations, sometimes termed **Monte Carlo models**, offer useful insights into the degree of variation that wildlife biologists and managers might expect to see over a long time. Monte Carlo simulation is central to the procedure known as population viability analysis, which we describe in Chapter 17.

8.7 Stability, cycles, and chaos

Paradoxically, the same density-dependent processes that are responsible for natural regulation can also induce population fluctuations, at least under special circumstances. One way that this can happen is when the maximum rate of growth is particularly high. For example, consider the dynamics of a hypothetical population whose maximum rate of increase $r_{\max} = 3.3$ and carrying capacity $K = 100$ (Fig. 8.17). In this case the population does not increase smoothly over time and level off at the carrying capacity, but rather the population fluctuates erratically over time, with no apparent repeated pattern. Such a pattern of population change is known as **deterministic chaos** (May 1976). It arises because the population grows so fast that it tends to overshoot the carrying capacity, a process known as **overcompensation** (May and Oster 1976). Once above the carrying capacity the net recruitment is negative

Fig. 8.17 Simulated dynamics over time of two different populations growing according to the Ricker logistic equation, with $r_{\max} = 3.3$ and $K = 100$. The first population was initiated at a density of 2.0 individuals per unit area, whereas the second population was initiated at a slightly higher density of 2.1 individuals per unit area. The rapid divergence in population dynamics due to slight changes in starting conditions is typical of deterministic chaos.

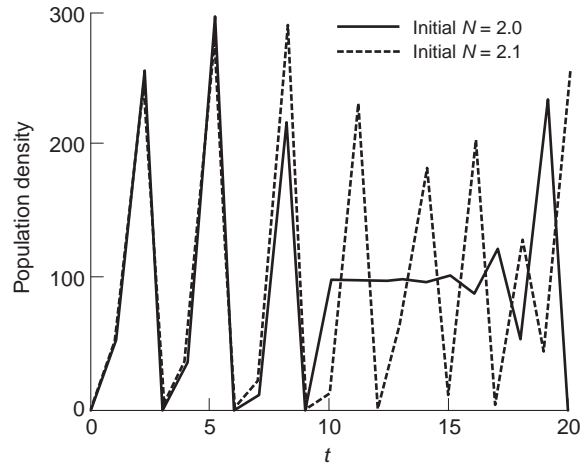
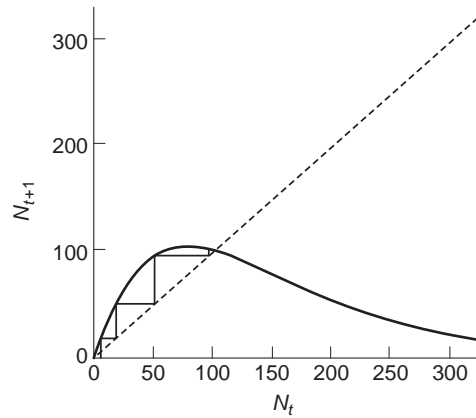


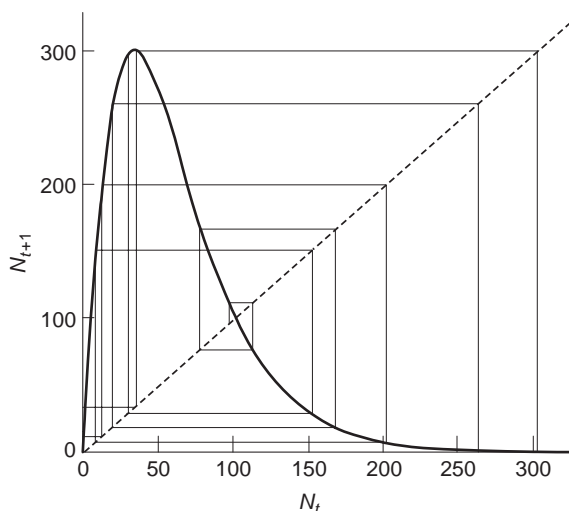
Fig. 8.18 Plot of predicted recruitment (N_{t+1}) relative to N_t (the heavy curve), equilibrium line at which $N_{t+1} = N_t$ (thin broken line), and trajectory of population dynamics over time for a simulated population following the Ricker logistic model, with $r_{\max} = 1.3$ and $K = 100$ (thin solid line).



(Fig. 8.13), so the population declines rapidly. Repetition of this boom–bust pattern of overshooting the carrying capacity and subsequent decline to levels below the carrying capacity results in the erratic fluctuations of deterministic chaos seen in Fig. 8.17. For lower rates of increase ($2.0 < r_{\max} < 2.7$) the pattern of fluctuation would be regular cycles, rather than deterministic chaos, but the underlying cause is still overcompensation.

The underlying cause of instability due to overcompensatory density dependence can be appreciated better by plotting the population dynamics over time on a graph with N_t on the horizontal axis and N_{t+1} on the vertical axis (Fig. 8.18). The diagonal identifies potential points of equilibria, at which $N_{t+1} = N_t$. We will also plot the recruitment curve. Dynamics are plotted by starting at a particular value of N_0 , projecting upwards to the recruitment curve, that identifies the next year's population density. Then we project horizontally to the broken equilibrium line, before repeating the process. At modest values of r_{\max} , the recruitment curve is low and has a shallow angle of incidence as it intersects the equilibrium line. The result is that the population trajectory becomes pinched between the recruitment curve and the equilibrium line as it converges on K . This leads to stability.

Fig. 8.19 Plot of predicted recruitment (N_{t+1}) relative to N_t (the heavy curve), equilibrium line at which $N_{t+1} = N_t$ (thin broken line), and trajectory of population dynamics over time for a simulated population following the Ricker logistic model, with $r_{\max} = 3.3$ and $K = 100$ (thin solid line).



Now, let us consider the pattern arising when $r_{\max} = 3.3$ (Fig. 8.19). The recruitment curve has a pronounced hump and intersects the equilibrium line at a sharp angle ($> 90^\circ$). The recruitment curve is so sharply peaked that recruitment events tend to overshoot the carrying capacity. This leads to the population collapsing to well below the carrying capacity, where the boom–bust cycle begins anew. In this way, the population never reaches an equilibrium, despite the fact that there is strong density dependence. This example demonstrates overcompensation, and it occurs when the angle of incidence of the recruitment curve exceeds 90° as it approaches the equilibrium line (May 1976; May and Oster 1976).

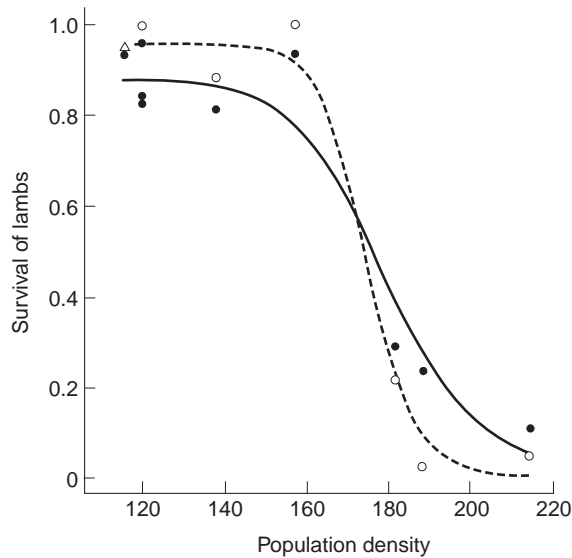
A diagnostic feature of deterministic chaos is that slight changes in starting conditions lead to quite different population dynamics over time. In Fig. 8.17, the simulated dynamics of the two hypothetical populations, started at slightly different densities, became quite different later on, illustrating their sensitivity to initial conditions. Both populations go through similar changes in the first few years but rapidly diverge thereafter, displaying different patterns of fluctuation.

Chaotic growth and fluctuation is unlikely for large wildlife species, which tend to have values of r_{\max} that are less than 0.5, well outside the parameter range in which cycles or chaos could arise through the simple mechanism we have described. Cycles or chaos can also arise, however, in other ways that are quite feasible for large wildlife species.

We have thus far limited our discussion to the simplest pattern of density dependence: linear changes in per capita rates of reproduction or survival. We saw earlier in the chapter (Figs 8.4 and 8.6) that there is no reason to expect natural regulation to be linearly density dependent. Some wildlife biologists have even argued that it may be the exception rather than the rule (Fowler 1981), and adult mortality in Serengeti wildebeest is a good example (Mduma *et al.* 1999).

Another example of non-linear demographic responses is seen in the feral Soay sheep on the St Kilda archipelago off the coast of Scotland. These sheep, similar in many ways to the ancestral sheep first domesticated by man, were initially introduced during the second millennium BC. They have roamed wild for several decades on several of the St Kilda islands, the best known of which is the small island of Hirta.

Fig. 8.20 Survival of Soay sheep lambs on the island of Hirta in relation to adult population density: females (solid line); males (broken line). (After Clutton-Brock *et al.* 1997.)



A fraction of the Hirta population uses an open, grassy area once occupied by people. Here the pregnant females use abandoned stone huts for shelter during birth. As a consequence, sheep numbers can be counted accurately and a large fraction of the newly born lambs can be caught and marked. Tracking these known individuals over the subsequent years has allowed unusually detailed calculations of age-specific reproduction and survival (Clutton-Brock *et al.* 1997).

The demographic pattern that has emerged from these field studies shows pronounced threshold effects of population density on sheep survival (Fig. 8.20). When the population is less than 200 adult sheep, survival of lambs, yearlings, and adults tends to be high: typically more than 90% in adults and yearlings and more than 80% in lambs. Increase in sheep abundance beyond the threshold tends to be accompanied by a precipitous decline in survival to low levels, sometimes as low as 10% (Fig. 8.20). Simulation models constructed with threshold survival and fecundity effects generate regular fluctuations of Soay sheep at 6-year intervals (Grenfell *et al.* 1992), qualitatively similar to the patterns seen in the real population (Figs 8.21–8.23). We show how to construct such a model in Box 8.1.

The model does not capture all of the variability in sheep abundance observed on St Kilda. Like all models, our age-structured model leaves out many important features. The model has no direct link with food supply or disease, both of which are important in shaping dynamics. Catastrophic mortality is largely caused by starvation, and vulnerability to starvation is exacerbated by high nematode infestation in the intestinal tract of individual sheep (Gulland 1992; Clutton-Brock *et al.* 1997). Perhaps more importantly, the model has no demographic or environmental stochasticity, which, as we have already seen, can considerably influence long-term dynamics. Using the Monte Carlo approach we outlined before, we could add such stochasticity.

Strong effects of weather variation can influence the population dynamics of Soay sheep (Grenfell *et al.* 1998; Coulson *et al.* 2001a). Populations of sheep on adjacent, isolated islands tend to be loosely synchronized, because they share a common climate (Grenfell *et al.* 1998). Although density-dependent processes regulate Soay

Fig. 8.21 Sigmoid survival functions in relation to the population density of adult+yearling Soay sheep, for adults (dashed-dotted line), yearlings (dotted line), and lambs (solid line), estimated by Clutton-Brock *et al.* (1997).

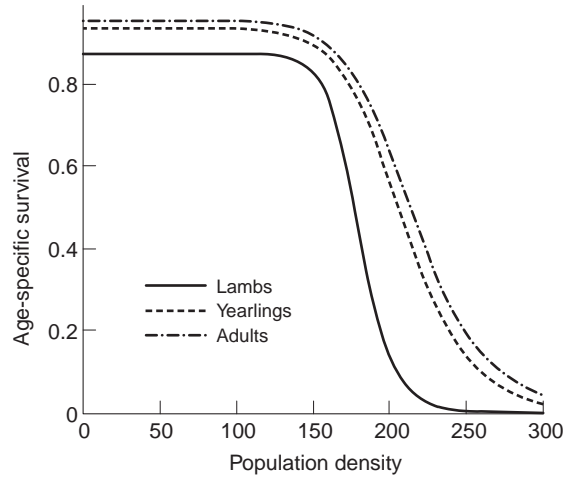


Fig. 8.22 Simulated dynamics of an age-structured population with sigmoid survival and fecundity functions with the same parameters as those of the Soay sheep population on the island of Hirta. (After Clutton-Brock *et al.* 1997.)

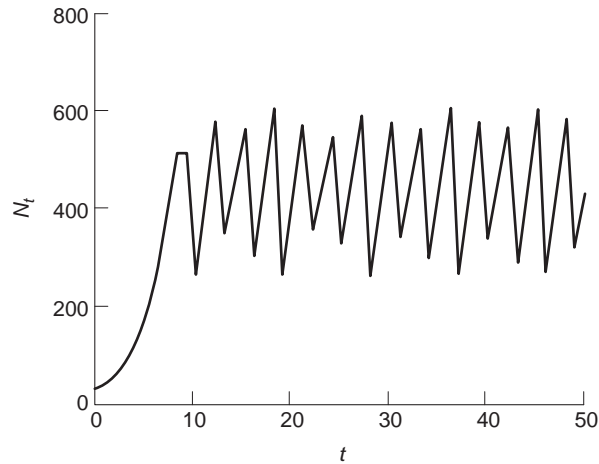
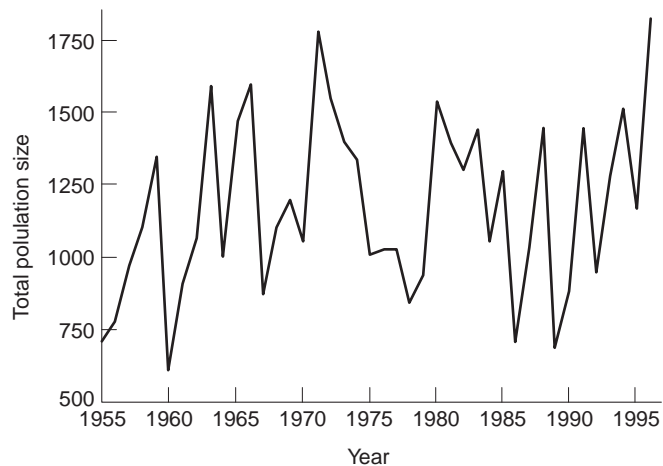


Fig. 8.23 Observed variation in the population of Soay sheep over the entire St Kilda archipelago. (After Clutton-Brock *et al.* 1997.)



Box 8.1 Model of the Soay sheep population on St Kilda.

Threshold effects on mortality can be well described by a sigmoid function:

$$\Psi(i, N) = \frac{\rho_{\max_i}}{1 + (\alpha_i N)^{\beta_i}}$$

where i refers to the age group (from 0 for newborns up to 2 for adults), N is population density of yearlings and adults, ρ_{\max} is maximum survival rate, and α and β are parameters determining the shape of the sigmoid survival function. Clutton-Brock *et al.* (1997) estimated the parameters of the Ψ function, from several years of data. These values are shown below:

$$\rho_{\max} = \begin{pmatrix} 0.88 \\ 0.94 \\ 0.96 \end{pmatrix}$$

$$\alpha = \begin{pmatrix} 0.00562 \\ 0.00484 \\ 0.00467 \end{pmatrix}$$

$$\beta = \begin{pmatrix} 15.3 \\ 9.46 \\ 8.93 \end{pmatrix}$$

By applying these sigmoid functions, we can mimic the threshold effect (Fig. 8.21).

Similar sigmoid functions can be fitted to age-specific fecundity rates of females:

$$\Omega(i, N) = \frac{m_{\max_i}}{1 + (\alpha\alpha_i N)^{\beta\beta_i}}$$

$$m_{\max} = \begin{pmatrix} 0.335 \\ 0.643 \\ 0.643 \end{pmatrix}$$

$$\alpha\alpha = \begin{pmatrix} 0.00629 \\ 0.00589 \\ 0.00589 \end{pmatrix}$$

$$\beta\beta = \begin{pmatrix} 24.1 \\ 14.1 \\ 14.1 \end{pmatrix}$$

By applying these density-dependent survival and fecundity rates to specific age classes, we can estimate changes in abundance over time:

$$\begin{pmatrix} n_0, t+1 \\ n_1, t+1 \\ n_2, t+1 \end{pmatrix} = \begin{pmatrix} \sum_i n_{i,t} \Omega\left(i, \sum_j n_{j,t}\right) \Psi\left(i, \sum_j n_{j,t}\right) \\ n_{0,t} \Psi\left(0, \sum_j n_{j,t}\right) \\ n_{1,t} \Psi\left(1, \sum_j n_{j,t}\right) + n_{2,t} \Psi\left(2, \sum_j n_{j,t}\right) \end{pmatrix}$$

sheep, the precise pattern of regulation is strongly affected by age structure. The mix of age groups on any of the islands is highly changeable, and slight modifications in age structure alter the dynamic consequences of density-dependent processes (Coulson *et al.* 2001a). The Soay sheep example illustrates how populations can fluctuate through a combination of (i) stochastic environmental effects; (ii) non-linear demographic responses; and (iii) delays that arise through a complex age structure.

8.8 Intraspecific competition

Regulation can occur by a number of mechanisms such as predation or parasitism, but a more common cause is competition between individuals for resources. Such resources can be food, shelter from weather or from predators, nesting sites, and space to set up territories. We have seen some examples already in Figs 8.9 and 8.10.

8.8.1 Definition

Intraspecific competition occurs when individuals of the same species utilize common resources that are in short supply; or, if the resources are not in short supply, competition occurs when the organisms seeking that resource nevertheless harm one or other in the process (Birch 1957).

8.8.2 Types of competition

When individuals use a resource so that less of it is available to others, we call this type of competition **exploitation**. This includes both removal of resource (consumptive use) when food is consumed and occupation of a resource (pre-emptive use) when resources such as nesting sites are used (see Section 12.3). Individuals competing for food need not be present at the same time: an ungulate can reduce the food supply of another that arrives later.

Another type of competition involves the direct interaction of individuals through various types of behavior. This is called **interference** competition. One example of behavioral interference is the exclusion of some individuals from territories. Another is the displacement of subordinate individuals by dominants in a behavioral hierarchy.

8.8.3 Intraspecific competition for food

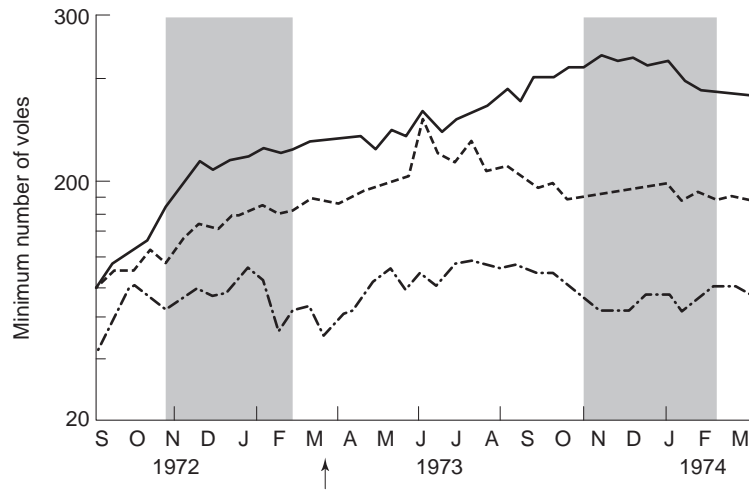
Experimental alteration of food supply

Food addition experiments provide the best evidence for intraspecific competition. Krebs *et al.* (1986) supplied extra food to snowshoe hares in winter from 1977 to 1985. This raised the mean winter density fourfold at the peak of the 10-year population cycle. Similarly, Taitt and Krebs (1981) increased the density of vole populations (Fig. 8.24) by giving them extra food. The elk population at Jackson Hole, Wyoming, is kept at a higher level than otherwise would be the case by supplementary feeding in winter (Boyce 1989). These examples show that food is one of the factors limiting density.

The dense shrubland (chaparral) of northern California contains two shrubs, chamise (*Adenostema taxiculatum*) and oak (*Quercus wislizenii*), that are preferred food for black-tailed deer (*Odocoileus hemionus*). These shrubs resprout from root stocks after burning to provide the new shoots which are the preferred food. Taber (1956) showed that on plots thinned by experimental burning, herbaceous food supply increased to 78 kg/ha from the 4.5 kg/ha found on control plots; and the shrub component increased to 460 kg/ha from 165 kg/ha. Deer densities consequently increased from 9.5/km² on the experimental controls to 22.9/km² on the treatment plots, while fertility of adult females increased from 0.77 to 1.65 young per female.

Red grouse (*Lagopus lagopus*) live year round on heather (*Calluna vulgaris*) moors in Scotland. Their diet consists almost entirely of heather shoots. Watson and Moss

Fig. 8.24 The numbers of Townsend's voles on trapping grids increase in proportion to the amount of food that is provided, indicating that intraspecific competition regulates the population. Control (dashed-dotted line); low food addition (dashed line); high food addition (solid line); shaded area indicates winter. (After Taitt and Krebs 1981.)



(1971) described experiments where some areas were cleared of grouse, fertilized with nitrogen in early summer, and then were left to be recolonized. Fertilizing increased the growth and nutrient content of heather. The size of their territories did not differ between fertilized and control areas when grouse set up their territories in fall. However, territorial grouse that had been present all winter reared larger broods on the fertilized than on the control areas, indicating that reproduction was affected by overwinter nutrition. Territory sizes did decline in the following fall and densities increased, showing the 1-year lag of density responding to nutrition. On other areas, old heather was burned every 3 years, creating a higher food supply of young regenerating heather. Territory size on these plots decreased (as density increased) in the same year as the treatment, so there was a more immediate response than on the fertilized plots.

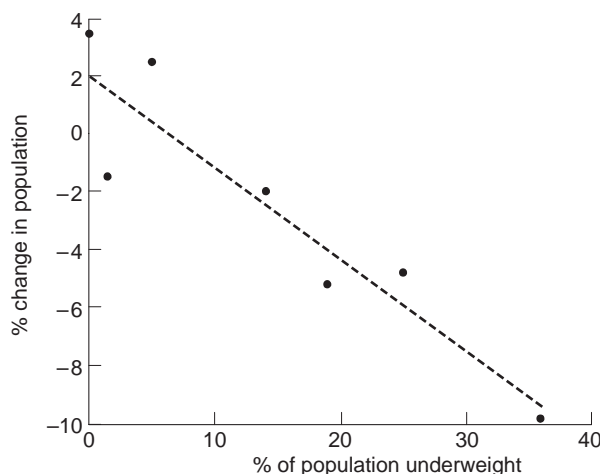
Direct measures of food

Snowshoe hare populations in the boreal forests of Canada and Alaska reach high numbers every 10 years or so. Measurements of known food plants, and feeding experiments, suggested that the animals ran short of food at peak numbers (Pease *et al.* 1979). Other measures such as the amount of body fat (Keith *et al.* 1984) and fecal protein levels (Sinclair *et al.* 1988) also identified food shortage at this time (see Section 4.9).

African buffalo graze the tropical montane meadows of Mt Meru in northern Tanzania, keeping the grass short. Grass growth rates and grazing offtake were measured by use of temporary enclosure plots. Growth in the rainy season was more than sufficient for the animals, but in the dry season available food fell below maintenance requirements (Sinclair 1977).

Murton *et al.* (1966) measured the impact of wood-pigeons (*Columba palumbus*) on their clover (*Trifolium repens*) food supply. Food supply was measured directly by counting clover leaves in plots. Pigeons consumed over 50% of the food supply during winter. They feed in flocks, those at the front of the flock obtaining more food than those in the middle or at the back. The proportion of underweight birds (< 450 g) was related directly to the overwinter change in numbers (Fig. 8.25) and

Fig. 8.25 The percentage change in a wood pigeon population in England is related to the proportion of the population that is underweight. (Data from Murton *et al.* 1966.)



inversely related to the midwinter food. Thus competition within flocks resulted in some animals starving, and the change in numbers was related to the proportion that starved.

Indirect measures of food shortage

Indirect evidence for competition for food comes from indices of body condition (see Section 4.9). The last stores of body fat that are used by ungulates during food shortages are in the marrow of long bones such as the femur. Bone marrow fat can be measured directly by extraction with solvents. However, since there is an almost linear relationship between fat content and dry weight (Hanks 1981) (see Section 4.9.3), it is easier to collect a sample of marrow from carcasses found in the field and oven dry it. A cruder but still effective method is to describe the color and consistency of the marrow, a method introduced by Cheatum (1949).

Other fat stores such as those around the heart, mesentery, and kidney are used up before the bone marrow fat starts to decline (see Section 4.9). The relationship between kidney and marrow fat holds for many ungulate species (see Fig. 4.11). If both kidney and marrow fat can be collected, a range of body conditions can be recorded. However, often the marrow fat is all that is found in carcasses because scavengers have eaten the internal organs.

Klein and Olson (1960) used bone marrow condition indices to conclude that deer in Alaska died from winter food shortage, as did Dasmann (1956) for deer in California. Similarly, migratory wildebeest in Serengeti that died in the dry season were almost always in poor condition, as judged by the bone marrow, and this was correlated with the protein level in their food (see Fig. 4.12). This dry season mortality was density dependent and was sufficiently strong to allow the population to level out (Sinclair *et al.* 1985; Mduma *et al.* 1999).

Problems with measurement of food supply

To determine whether competition for resources such as food is the cause of regulation we need to know what type of food is eaten, how much is needed, and how much is available. What is needed must exceed what is available for competition to occur. The types of food eaten form the basis for many studies on diet selection,

sometimes called **food habit studies**. These in themselves do not tell us what is needed in terms of digestible dry matter, protein, and energy. We should note that such requirements are unknown for most wild species and we have to use approximations from other, often domestic, species. The amount of food available to animals is particularly difficult to assess because we are unlikely to measure potential food in the same way as does an animal. For example, animals are likely to be far more selective than our crude sampling and so we are likely to record more “food” than the animal sees. Our measures of food supply are often seriously flawed, and this is one of the reasons why direct evidence for intraspecific competition for food is rare. There is far more indirect evidence for competition provided by indicators such as body condition.

8.9 Interactions of food, predators, and disease

The effect of limited food on population demography can go beyond the direct effects of undernutrition. There can also be synergistic interactions with predation and disease. Animals may alter their behavior when food becomes difficult to find in safe areas, searching increasingly in areas where they are at risk of predation in order to avoid eventual starvation (McNamara and Houston 1987; Lima and Dill 1990). This is called **predator-sensitive foraging** and has been observed in snowshoe hares (Hik 1995; Hodges and Sinclair 2003). Such behavior can result in increased predation well before starvation takes effect, as seen in wildebeest (Sinclair and Arcese 1995).

Disease can also interact synergistically with food, pathological effects suddenly becoming apparent at a certain, sometimes early, stage of undernutrition (see Chapter 11). Sometimes food, disease, and predators all interact. Wood bison numbers in the Wood Buffalo National Park, Canada, switch suddenly from a high-density food-regulated state to a low-density predator-regulated state when diseases, such as tuberculosis and brucellosis, affect the population (Joly and Messier 2004).

8.10 Summary

Regulation is a biotic process which counteracts abiotic disturbances affecting an animal population. Two common biotic feedback processes are predation and intraspecific competition for food. These are called density-dependent factors if they act as negative feedbacks. Negative feedback imparts stability to the population. Disturbances are provided by fluctuating weather or other environmental conditions (termed environmental stochasticity) or chance effects on reproduction and survival (termed demographic stochasticity). They are called density-independent factors and will cause populations to drift to extinction if there are no counteracting density-dependent processes operating. For wildlife management it is necessary to know (i) what are the causes of the density-dependent processes that stabilize the population, and what are the causes of fluctuations and instability; and (ii) which age and sex groups are most influenced by these stabilizing or destabilizing processes.

One way to understand such effects is to model density-dependent changes in population growth rate, using logistic models. Application of such models shows that whereas density dependence is often stabilizing, overcompensatory density dependence can itself encourage population fluctuation, beyond the degree we would expect due to demographic or environmental stochasticity. A common cause of regulation is intraspecific competition for food.

Competition occurs if the needs of the population exceed availability. To measure such competition we need to know how much food is available and how much is needed, and whether it is density dependent. Food can also interact with predation and disease to regulate populations.

9 Competition and facilitation between species

9.1 Introduction

Species do not exist alone. They live in a community of several other species and some of these will interact. There are various forms of interaction between species; competition, commensalism (facilitation), mutualism (symbiosis), predation, and parasitism are the main ones. These are defined by the way each species affects the other, as is shown in Table 9.1. In competition each species suffers from the presence of the other, although the interaction need not be balanced. With commensalism or facilitation one species benefits without affecting the other, while in mutualism both benefit. These can be thought of as the converse of interspecific competition. With predation and parasitism one species benefits to the disadvantage of the other. We shall discuss predation in Chapter 10 and parasitism in Chapter 11 and will confine ourselves here to interspecific competition and mutualism.

9.1.1 Definition

Interspecific competition is similar to intraspecific competition. It occurs when individuals of different species utilize common resources that are in short supply; or, if the resources are not in short supply, competition occurs when the organisms seeking that resource nevertheless harm one or other in the process (Birch 1957).

9.1.2 Implications

Interspecific competition deals with the cases when there are two or more species present, and we should be aware of a number of implications arising from this definition.

1 Competition must have some effect on the fitness of the individuals. In other words, resource shortage must affect reproduction, growth, or survival, and hence the ability of individuals to get copies of their genes into the next generation.

2 Although it is necessary for species to require common resources (i.e. overlap in their requirements), we cannot conclude there is competition unless it is also known that the resource is in short supply, or that they affect each other.

3 The amount of resource such as food that is available to each individual must be affected by what is consumed by other individuals. Thus two species cannot compete if they are unable to influence the amount of resource available to the other species, or to interfere with that species obtaining the resource.

Table 9.1 Types of interaction.

Species 2	Species 1		
	+	0	–
+	Mutualism	Commensalism	Predation/parasitism
0	Commensalism	Competition	(Amensalism) Competition
–	Predation/parasitism		Competition

4 Both exploitation and interference competition (see Section 8.8.2) can occur between species, although interference between species is relatively uncommon.

9.2 Theoretical aspects of interspecific competition

To obtain an understanding of what might be the expected outcome from a simple and idealized interspecific competition we return to the logistic equation:

$$dN_1/dt = r_{m1} \times N_1 \times (1 - N_1/K_1) \quad (9.1)$$

9.2.1 Graphical models

The term in parentheses $(1 - N_1/K_1)$ describes the impact of individuals upon other individuals of the same species and on the population growth rate dN_1/dt . We must now add a term representing the impact of the second species N_2 on species 1. The equation for the effect of species 2 on population growth of species 1 is:

$$dN_1/dt = r_{m1} \times N_1 \times (1 - N_1/K_1) \times (a_{12} \times N_2/K_1) \quad (9.2)$$

where r_{m1} is the intrinsic rate of increase for species 1.

The ratio N_2/K_1 represents the abundance of species 2 relative to the carrying capacity (K_1) of species 1. It is a measure of how much of the resource is used by species 2 that would have been used by species 1. The **coefficient of competition** a_{12} measures the competitive effect of species 2 on species 1. If we define the competitive effect of one individual of species 1 upon the resource use of an individual of its own population as unity, then the coefficient for the effect of other species is expected to be less than unity. We expect this because individuals will compete more strongly with those similar to themselves than with the dissimilar individuals of other species. This does not always occur: when two species differ greatly in size an individual of the larger species (l) may consume far more of a resource than one of the smaller species (s) and in this case the a_{sl} could be greater than unity. The converse effect of species 1 on species 2 is denoted by the coefficient a_{21} in the equation for the other species:

$$dN_2/dt = r_{m2} \times N_2 \times (1 - N_2/K_2) \times (a_{21} \times N_1/K_2) \quad (9.3)$$

These two equations (9.2, 9.3) are called the Lotka–Volterra equations, after the two authors who produced them (Lotka 1925; Volterra 1926a). We can examine the implications of the equations graphically by plotting the numbers of species 2 against those of species 1, as in Fig. 9.1a. First we plot the conditions for species 1 when dN_1/dt is zero. There are the two extreme points when N_1 is at K_1 so that N_2 is zero, and when N_1 is zero because species 2 has taken all the resource. This latter point can be found from eqn. 9.2 by setting dN_1/dt to zero and rearranging so that it simplifies to:

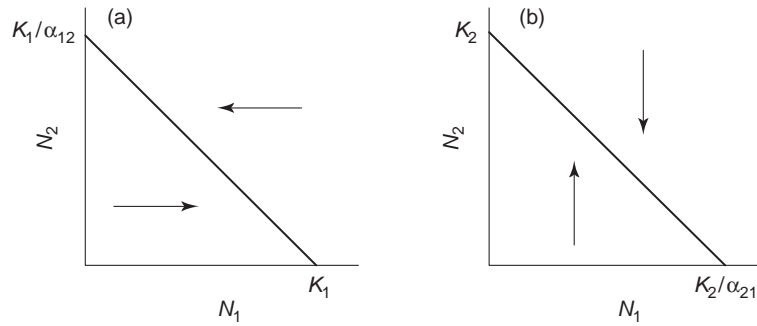
$$N_1 = K_1 - a_{12} \times N_2$$

If the resource is taken entirely by species 2, then:

$$N_1 = 0, \text{ and } N_2 = K_1/a_{12}$$

Of course there can be any combination of N_1 and N_2 so that dN_1/dt is zero; this is seen from the diagonal line joining these two extreme points. To the left of this line

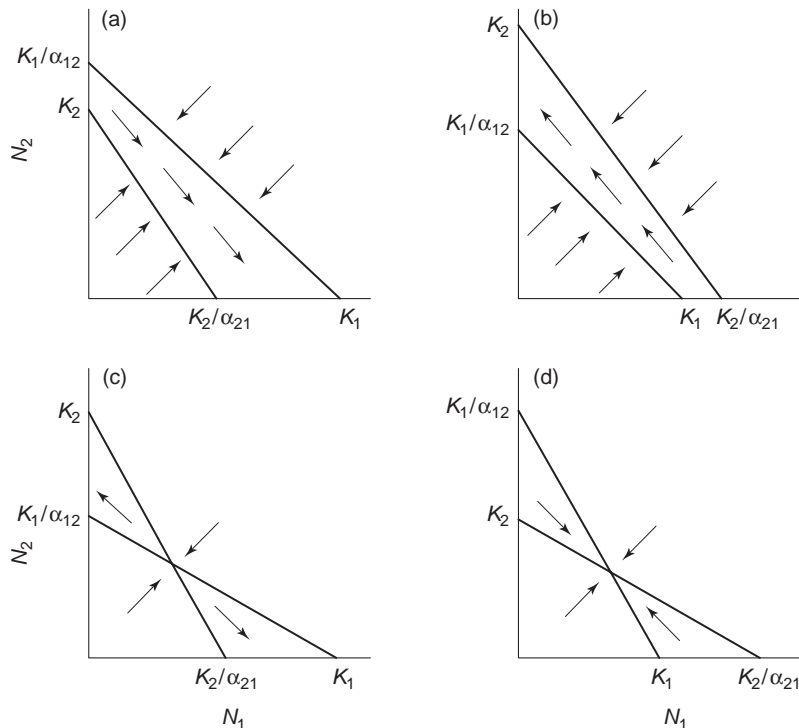
Fig. 9.1 Isoclines for the Lotka–Volterra equations. (a) At any point on the isocline $dN_1/dt = 0$. This indicates where the number of species 1 is held constant for different population sizes of species 2. Species 1 increases to the left of the isocline, but decreases right of it. (b) The isocline where $dN_2/dt = 0$. This shows where the population of species 2 is held constant at different values of species 1. Species 2 increases below the line, but decreases above it.



dN_1/dt is positive so that N_1 increases, and to the right it is negative and N_1 decreases as indicated by the arrows. At all points on the line (called an **isocline**) the population is stationary. Exactly similar reasoning produces the equivalent diagram for species 2 (Fig. 9.1b). Below the line (isocline) N_2 increases, and above it N_2 decreases.

With these two diagrams describing the competitive abilities of the two species independently we can now predict the outcome of competition between them. If we put the two diagrams in Fig. 9.1 together, as in Fig. 9.2a, we see that K_1 is larger than K_2/α_{21} . The latter term is the number of species 1 required to drive species 2 to extinction, and since it is possible for species 1 to exist at higher numbers than this level (i.e. at K_1), species 1 will drive species 2 down. On the other axis we see that

Fig. 9.2 The relationship of the two species' isoclines determines the outcome of competition. (a) Species 1 increases at all values of species 2 so that species 1 wins. (b) The converse of (a) such that species 2 wins. (c) In the region where the isocline of species 1 is outside that of species 2, species 1 wins and vice versa, so that either can win. (d) A stable equilibrium occurs because all combinations tend towards the intersection of the isoclines.



K_2 , which is the maximum number of species 2 that the environment can hold, is less than that necessary to drive down species 1. Therefore species 2 always loses when the two species occur together, as can be seen by the resultant arrows and by the fact that the species 1 isocline is always outside that of species 2.

The above outcome is not the only possible solution, for this depends on the relative positions of the two isoclines that are shown in Figs 9.2b–d. Figure 9.2b is the converse to that of Fig. 9.2a so that species 2 always wins. In Fig. 9.2c we see that $K_2 > K_1/a_{12}$ and $K_1 > K_2/a_{21}$ so that, depending on the exact combination of the two population sizes, either can win. Where the two isoclines cross there is an equilibrium point but this is unstable in the sense that any slight change in the populations will cause the system to move to either K_1 or K_2 and the extinction of one of the species. In nature we would never see such an equilibrium.

Figure 9.2d also shows the two isoclines crossing, but in this case $K_2 < K_1/a_{12}$ and $K_1 < K_2/a_{21}$ (i.e. individuals of the same species affect each other more than do individuals of the other species, and neither is capable of excluding the other). This also means that intraspecific competition is always greater than interspecific competition. Hence, whatever the combination of the two populations, the arrows show that the system moves to the equilibrium point, which is therefore stable. This situation can occur only if there is some form of separation in the resources that they use, which we call niche partitioning (see Section 9.6).

9.2.2 Implications and assumptions

1 We can see from the figures that the outcome of competition depends upon the carrying capacities (K_1 and K_2) and the competition coefficients (a_{12} and a_{21}) according to the Lotka–Volterra model. The intrinsic rate of increase has no influence on which species will be the eventual winner.

2 Coexistence occurs when intraspecific competition within both species is greater than interspecific competition between them.

3 These equations can be expanded to include the effects of several species on species 1 by summing the $a \times N$ terms. This assumes that each species acts independently on species 1.

4 There are several other assumptions underpinning the logistic equation, for example constant environmental conditions leading to constant r and K , and no lags in competing species' responses to each other. Furthermore, the competition coefficients are constant: the intensity of competition does not change with size, age, or density of the competing species.

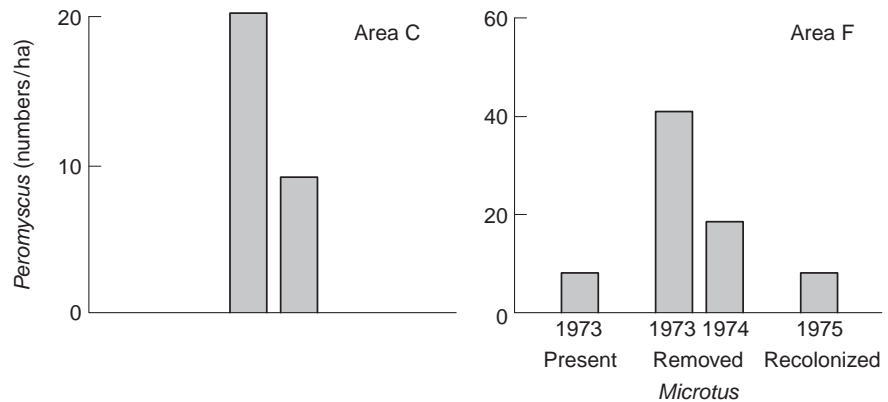
These assumptions mean that the Lotka–Volterra equations, like the logistic one, are simplistic and idealized. It is unlikely that the assumptions hold, although they may be approximated in some cases. The real value of these models is that they show how it is possible for coexistence to occur in the presence of competition, and that exclusion is not necessarily predetermined but may depend on the relative densities of the competing species.

9.3 Experimental demonstrations of competition

9.3.1 Perturbation experiments

Much of the work in ecology has assumed that competition has occurred and is necessary for the coexistence of species, and competition is one of the major assumptions in Darwin's theory of natural selection. Nevertheless, it is necessary to demonstrate that interspecific competition does actually take place. One of the most direct approaches is to carry out a **removal experiment** whereby one of the species is removed, or reduced in number, and the responses of the other species are then

Fig. 9.3 Population densities of deer mice (*Peromyscus*) on two areas from which voles (*Microtus*) were removed in the years 1973 and 1974. On area F only deer mice were monitored after voles were allowed to recolonize. Deer mice were absent or in low numbers before and after the vole removal, but high during the removal. (Data from Redfield *et al.* 1977.)



recorded. If competition has been operating we would expect that either the population, or reproductive rate, or growth rate of the other species would increase.

Forsyth and Hickling (1998) showed from an incidental removal experiment through hunting that Himalayan tahr (*Hemitragus jemlahicus*) are associated with declining populations of chamois (*Rupicapra rupicapra*). Competition appears to occur through behavioral interference, with the larger tahr excluding chamois. Another experiment, illustrated in Fig. 9.3, examined the competitive effect of voles (*Microtus townsendii*) on deer mice (*Peromyscus maniculatus*). Deer mice normally live in forests but one race on the west coast of Canada can also live in grassland, the normal habitat of voles. Redfield *et al.* (1977) removed voles from three plots and compared the population response of the deer mice there with that on two control areas. On one control there were no deer mice, on the other 4.7/ha. All the removal areas showed increases in deer mouse numbers, one going from 7.8/ha before removal to 62.5/ha 2 years later. At the end of the study, when the workers stopped removing voles, these animals recolonized, reaching densities of 109/ha, while deer mice numbers dropped to 9.4/ha. In another experiment, instead of removing voles, Redfield disrupted the social organization of the voles by altering the sex ratio so that there was a shortage of females, but the density remained similar to the controls. In this area deer mice numbers increased from nearly zero to 34/ha. This result suggests that it was **interference competition** due to aggression from female voles that excluded the deer mice because the density and food supply remained the same.

A similar type of experiment was conducted on desert rodents in Arizona by Munger and Brown (1981). They excluded larger species from experimental plots while smaller species were allowed to enter. Plots were surrounded by a fence, and access was controlled by holes cut to allow only the smaller species to enter. There were two types of small rodents, those that ate seeds (granivores) and those that ate a variety of other foods as well (omnivores). Munger and Brown predicted that if there was exploitation competition for seeds between the large and small granivores then the latter should increase in number in the experimental plots, while the omnivore populations should stay the same; if, however, the increased density of granivores was an artifact of the experiment (e.g. by excluding predators) then the number of small omnivores should also increase. Figure 9.4 shows that after a 1-year delay small granivores reached and maintained densities that averaged 3.5 times higher on the removal plots than on the controls, but the small omnivores did not show any significant

Fig. 9.4 Exclusion of large granivorous rodents resulted in an increase in the small granivorous rodent population relative to control areas, indicating competition. Small omnivorous rodent numbers did not increase significantly, indicating lack of competition. (Data from Munger and Brown 1981.)

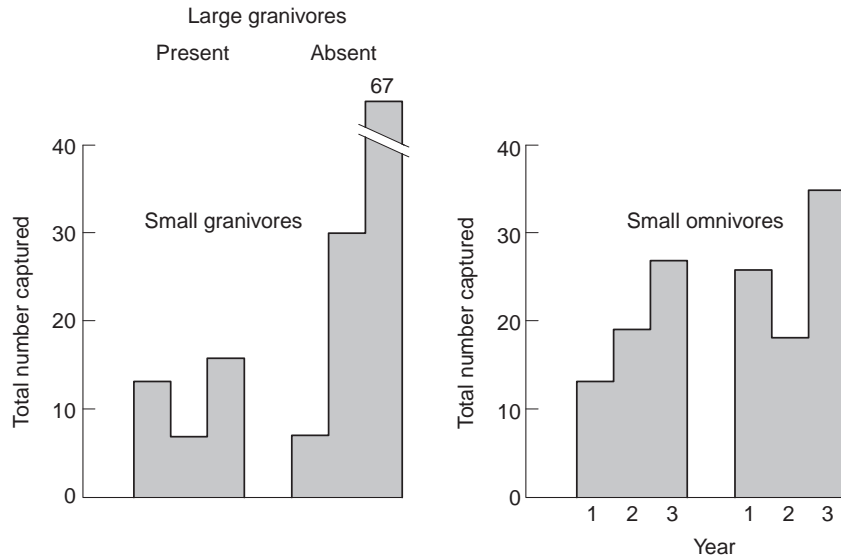
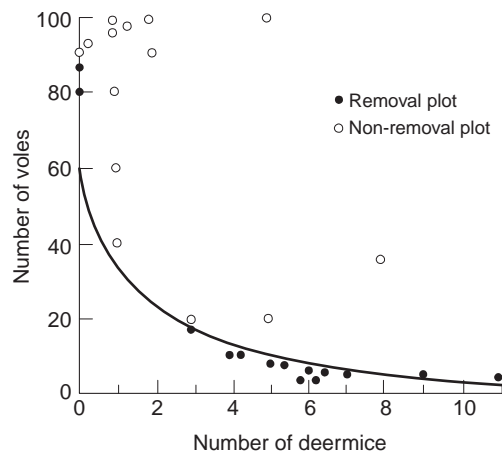


Fig. 9.5 Number of deer mice (*Peromyscus maniculatus*) known to be alive at time t plotted against number of voles (*Microtus ochrogaster*) known to be alive at time $t - 1$ ($t - 1$ is the sample period 2 weeks earlier than period t). (After Abramsky *et al.* 1979.)



increase. These results are consistent with the interpretation that there was competition between large and small granivorous rodents.

Although the above examples produced results consistent with the predictions of interspecific competition, there was no attempt to measure the competition coefficients. However, Abramsky *et al.* (1979) carried out a similar removal experiment on the shortgrass prairie in Colorado in which a competition coefficient was measured. In this case voles (*M. ochrogaster*) were removed and the response of deer mice (*P. maniculatus*) recorded. Figure 9.5 shows the negative relationship between the number of deer mice present in the removal plot and the number of voles present in the previous sampling period 2 weeks earlier, as expected if competition were acting. To measure the competition effect (a) of voles on deer mice, the Lotka–Volterra equation was used. At equilibrium $dN_1/dt = 0$, and so:

$$K_1 = N_1 + a \times N_2 \times (2^{0.75})$$

where K_1 is the carrying capacity of the environment for individuals of deer mice when alone, N_1 is the number of deer mice, N_2 is the number of voles, and $2^{0.75}$ is the conversion factor, and standardizes the species in terms of their metabolic rates.

The body weight (W) of voles is about two times that of deer mice, and the basal metabolic rate (M) is taken as $M = W^{0.75}$ (see Section 4.5.2). Using various combinations of N_1 and N_2 an average estimate of $a = 0.06$ was obtained.

Properly designed removal experiments are difficult to carry out for practical reasons, so it is not surprising that they have not yet been performed with large mammals.

9.3.2 Natural experiments

An easier approach uses natural absences or combinations of species to observe responses that would be predicted from interspecific competition. For example, mallard ducks (*Anas platyrhynchos*) breed on oligotrophic (low nutrient) lakes in Sweden (Pehrsson 1984). Some of the lakes contained fish while others did not. In lakes with fish, the density of mallards was lower, mean invertebrate food size was lower, and emerging insects were significantly smaller. In an experiment where ducklings were released, their intake rate was higher on lakes without fish (Table 9.2). These results imply competition between ducks and fish.

Another type of natural experiment is illustrated by the distributions of two gerbilline rodent species in Israel (Abramsky and Sellah 1982). One species, *Gerbillus allenbyi*, lives in coastal sand dunes and is bounded in the north by Mt Carmel. In the same region the other species, *Meriones tristrami*, is restricted to non-sandy habitats. In the coastal area north of Mt Carmel, *M. tristrami* occurs alone and inhabits several soil types including the sand dunes. Abramsky and Sellah suggested that *M. tristrami* colonized from the north and was able to bypass Mt Carmel, whereas *G. allenbyi* colonized from the south and could not pass the Mt Carmel barrier. In the region of overlap, south of the barrier, interspecific competition had excluded *M. tristrami* from the sand dunes. They tested this hypothesis by removing *G. allenbyi* from habitats where the two species overlapped, and found that there was no significant increase in *M. tristrami*. They concluded that there was no present-day competition occurring. Instead they suggested that competition in the past had resulted in a shift in habitat choice so that there was no longer any detectable competition.

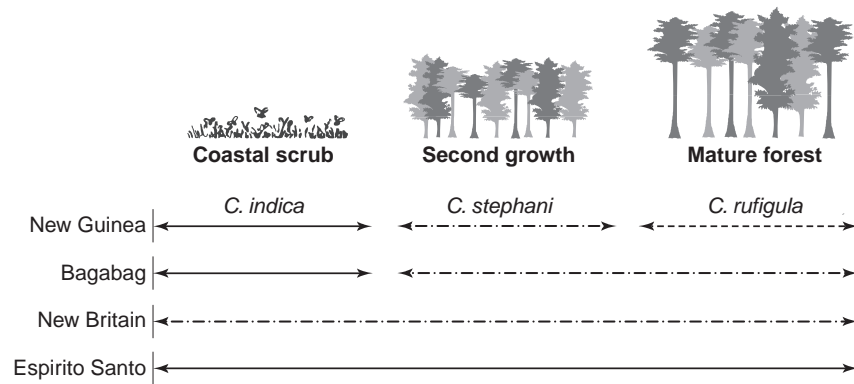
Islands are sometimes used to look at the distributions of overlapping species, because on some islands a species can occur alone while on others it overlaps with related species. The theory of interspecific competition would predict that when alone a species would expand the range of habitats it uses (a process we call **competitive release**), while on islands where there are several species the range of habitats contracts

Table 9.2 Mean dry weight of subaquatic invertebrates available to mallard ducklings and the rate of duckling food intake in Calnes with and without fish in Sweden.

	Year	Lakes without fish	Lakes with fish
Mean dry weight (May–June)	1977	119.8 (21.0)	45.3 (13.7)**
	1978	159.0 (9.9)	26.5 (4.8)**
Duckling feeding (food items/min)	1977	12.4 (0.6)	9.5 (0.5)***
	1978	20.4 (5.1)	7.9 (0.7)**

** $P < 0.01$; *** $P < 0.001$.
From Pehrsson (1984).

Fig. 9.6 Habitats of ground doves (*Chalcophaps* and *Gallicolumba*) on islands off New Guinea demonstrate “competitive release.” (After Diamond 1975.)



(competitive exclusion). A good example of this is seen in ground doves on New Guinea and surrounding islands (Diamond 1975). On the larger island of New Guinea there are three species each with its own habitat (Fig. 9.6): *Chalcophaps indica* in coastal scrub, *C. stephani* in second growth forest further inland, and *Gallicolumba rufigula* in the interior rainforest. On the island of Bagabag *G. rufigula* is absent and *C. stephani* expands into the mature forest. On some islands (New Britain, Karkar, Tolokiwa) only *C. stephani* occurs and it uses all habitats, while on the island of Espirito Santo only *C. indica* occurs and this species also expands into all habitats. It is assumed that this habitat expansion has been due to competitive release through the absence of the other potential competitors.

9.3.3 Interpreting perturbation experiments

Perturbation experiments are designed to measure responses of populations that would be predicted from interspecific competition theory. We should be aware, however, that there are two types of perturbations (Bender *et al.* 1984). One, called a **pulse** experiment, involves a one-time removal of a species. We then measure the rate of return by the various species to the original equilibrium. This requires accurate measurements of rates of population increase, which in practice is not easy and in fluctuating environments very difficult. As a consequence few of these experiments are carried out.

The other type of perturbation is the continuous removal, or **press**, experiment. Let us assume that species 1 is reduced to a new level and kept there. Other species are allowed to reach a new equilibrium and it is this level that is observed. This type of perturbation avoids having to measure rates but there are other problems. If there are more than two species in a community, which in most cases there are, an increase in another species' population is neither a necessary nor sufficient demonstration of competition. First, species 1 and species 2 may not overlap, and so not compete, but they may affect each other through interactions with other competing species: this is **indirect competition**. Second, the two species could be alternative prey for a food-limited predator. Changes in the population of species 1 could affect that of species 2 by influencing the predator population: this has been termed **apparent competition** (Holt 1977) and we will discuss it again below (see Section 9.8).

All of the examples we have discussed above are press experiments and strictly speaking, in order to demonstrate competition unequivocally, we would need to know that: (i) resources were limiting; (ii) there was overlap in the use of the resources; (iii) other potential competitors were having a negligible effect; and (iv) predator

populations were not responding to the experiment. In few cases have all these conditions been met. Because of these difficulties an entirely different approach to the study of interspecific competition has measured the pattern of overlap in the use of resources. We now consider this approach.

9.4 The concept of the niche

In Chapter 3 we saw that different species on different continents appeared to adopt the same role in the community and often these species have evolved similar morphological and behavioral adaptations. This place in the community is called the **niche**, defined by Elton (1927) as the functional role and position of the organism in its community. (We provide the modern definition later.)

For practical reasons the niche has come to be associated with use of resources. Thus, we can plot the range and frequency of seed sizes eaten by different bird species, as a hypothetical example, in Fig. 9.7a. Species that exploit the outer parts of the

Fig. 9.7 (a) Hypothetical frequency distribution of seeds of different sizes indicating the range and overlap of potential niches for granivores. (After Pianka *et al.* 1979.) (b) Range of seed sizes eaten by British finches feeding on herbaceous plants. Seeds are in five size categories A to E. The finches are redpoll (*Carduelis flammea*), linnet (*C. cannabina*), greenfinch (*Chloris chloris*), and hawfinch (*Coccothraustes coccothraustes*). (After Newton 1972.)

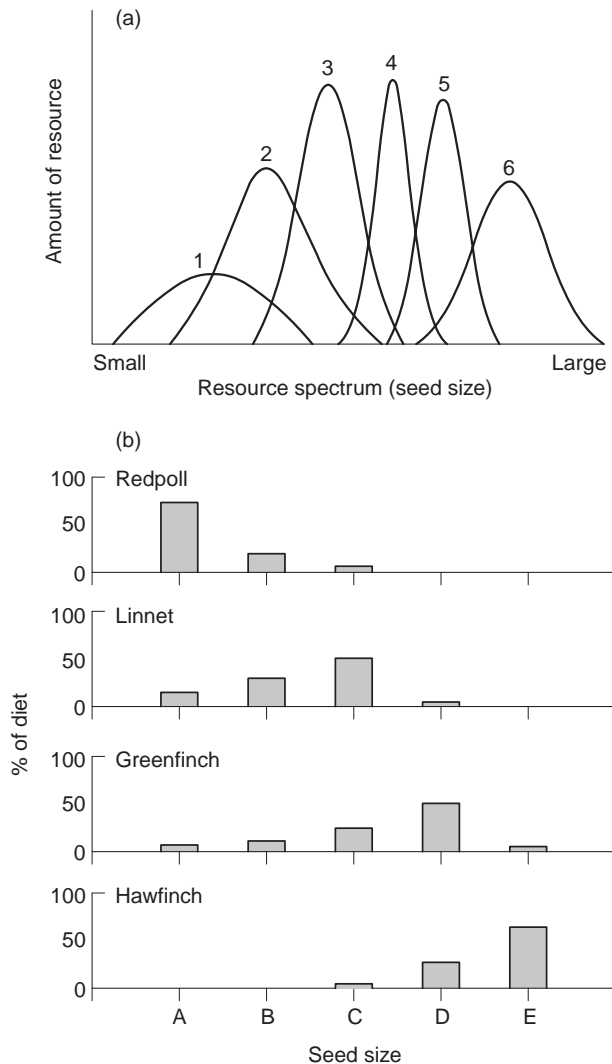
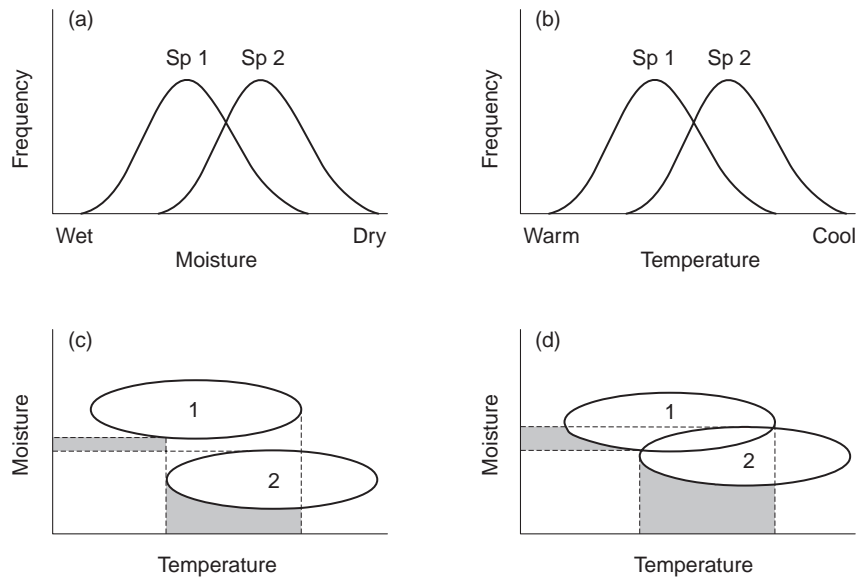


Fig. 9.8 Hypothetical frequency distribution of species 1 and species 2 along two parameter gradients: (a) moisture; (b) temperature. Outline of the species distributions when considering the two parameters simultaneously shows niches that can be either distinct (c), or overlapping (d).

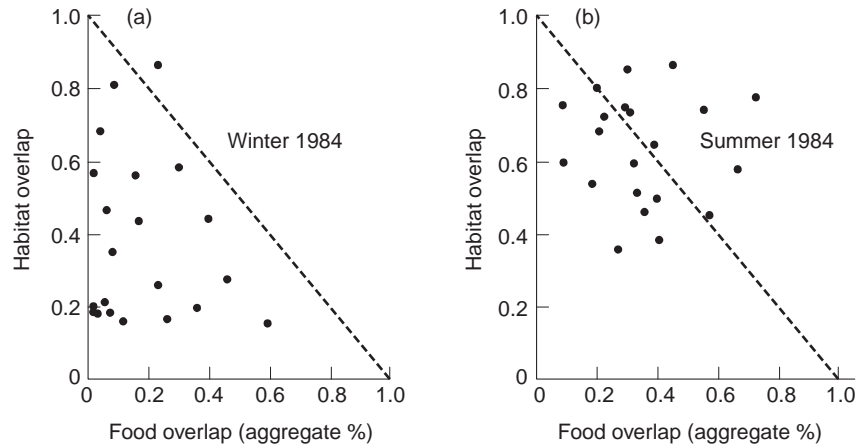


resource spectrum use a broader range of resources because they are less abundant. Some species, for example 2, 3, and 4, overlap while others such as 2 and 5 do not. Overlap is necessary (but not sufficient) to demonstrate competition. An example (Fig. 9.7b) is provided by the range of seed sizes eaten by finches in Britain (Newton 1972). In this case we see that, contrary to the theoretical distribution proposed in Fig. 9.7a, there is a broader range of seed sizes eaten by these finches in the middle range than by birds eating seeds at the extremes.

So far we have considered only one resource axis, that is, one variable such as seed size. When we consider two or more axes the picture becomes less clear cut in terms of overlap. Take two species, 1 and 2, which overlap along two axes, for example moisture and temperature as in Figs 9.8a and 9.8b. If we plot the outline of the two species distributions by considering the two axes simultaneously we see that it is possible for the two distributions to be distinct (Fig. 9.8c) or to overlap (Fig. 9.8d). Which one occurs depends on whether individuals show **complementarity** (i.e. individuals that overlap on one axis do not do so on the other one (Fig. 9.8c), or overlap simultaneously on both axes (Fig. 9.8d)).

An example of complementarity is shown in Fig. 9.9. DuBowy (1988) examined the resource overlap patterns in a community of seven North American dabbling ducks all of the genus *Anas*, by plotting habitat overlap against food overlap for pairs of species. In winter, when it is assumed that resources were limiting, points for pairs were below the diagonal line (Fig. 9.9a), indicating complementarity: pairs with high overlap in one dimension had low overlap in the other. In contrast, during summer species pairs showed high resource overlap in both dimensions (several points are outside the line), indicating that species fed on the same food at the same place. In summary, the change in niche of these duck species from summer to winter results in lower overlap and by implication lower competition at a time when we would expect that resources would be limiting. Note, however, that neither the lack of resources nor interspecific competition was demonstrated, merely that the results conform to what we would predict if competition had been acting.

Fig. 9.9 Resource overlaps in seven species of dabbling ducks. Below the broken line there is complementarity in overlaps. (a) In winter, high habitat overlap between pairs of species tends to be associated with low food overlap, demonstrating complementarity. (b) In summer there is simultaneous overlap in both dimensions. (After DuBow 1988.)



Green (1998) found complementarity in ducks along habitat and feeding behavior axes. He found in dabbling and diving ducks in Turkey that pairs with similar habitat had dissimilar feeding mechanisms.

We have considered only two dimensions of a niche so far, but clearly the niche must include every aspect of the environment that would limit the distribution of the species. We cannot draw all these dimensions on a graph but we could perhaps imagine a sort of sphere or volume with many dimensions, which could theoretically describe the complete niche. Hutchinson (1957) described this as the *n-dimensional hypervolume*. This is the fundamental niche of the species and is defined by the set of resources and environmental conditions that allow a single species to persist in a particular region (Schoener 1989; Leibold 1995). This suggests that the niche is in some way discrete. However, resource measures are usually continuous so the discreteness does not come from these. Rather it comes from the constraints of the species in terms of their morphology, physiology, and behavior – a species is more efficient at using some combinations of a resource than other combinations, while other species have different combinations where they are most efficient. These peaks of efficiency, then, are the adaptive peaks exhibited by a species (Schluter 2000).

The fundamental niche is rarely if ever seen in nature because the presence of competing species restricts a given species to a narrower range of conditions. This range is the observed or **realized niche** of the species in the community. It emphasizes that interspecific competition excludes a species from certain areas of its fundamental niche. In terms of the Lotka–Volterra diagrams (see Fig. 9.2) the weaker competitor has no realized niche in Figs 9.2a and 9.2b, and for Fig. 9.2d parts of the fundamental niche are not used.

The difference between the two types of niches can be seen in a study by Orians and Willson (1964) of red-winged blackbirds (*Agelaius phoeniceus*) and yellow-headed blackbirds (*Xanthocephalus xanthocephalus*). Both species make their nests among reeds in freshwater marshes of North America, and, if alone, both will use the deep-water parts of the marsh (there is greater protection from mammalian predators here). However, when the two species occur together, the yellow-heads exclude the red-winged blackbirds, which are then restricted to nesting in the shallow parts. Thus, the fundamental niche for nesting red-winged blackbirds is the whole marsh, but the

realized niche is the shallow-water reedbed. Coexistence occurs from the partitioning of the resource (nesting habitat), and the divergence of realized niches.

9.5 The competitive exclusion principle

In 1934 Gause stated that “as a result of competition two species hardly ever occupy similar niches, but displace each other in such a manner that each takes possession of certain kinds of food and modes of life in which it has an advantage over its competitor” (Gause 1934). In short, two species cannot live in the same niche, and if they try one will be excluded; second, coexisting species live in different niches. This is known as the **principle of competitive exclusion**, or Gause’s principle (Hardin 1960), and has become one of the fundamental tenets of ecology. It proposes that species can coexist if adaptations arise to effectively partition resources. Examples of such adaptations include the use of different microhabitats, different components of prey, different ways of feeding, different life stages of the same prey, different time periods in the same habitat, or taking advantage of disturbance, and interference competition (Richards *et al.* 2000). Therefore, Gause’s principle has become the basis for studies of resource partitioning and overlap as a way of measuring interspecific competition.

There are, however, two serious problems with Gause’s statement. The first is that it is a trivial truism, because we have already identified the two coexisting populations as being different by calling them different species, and, therefore, if we look hard enough we are likely to find differences in their ecology as well. This is called a tautology: having defined the species as being different, it should be no surprise to find they are different.

The second problem is that the principle is untestable. It cannot be disproved because either result (exclusion or coexistence) can be attributed to the principle. To disprove the principle it is necessary to demonstrate that the niches of two species are identical. Yet, as we can see from Fig. 9.8, what appears to be overlap, even complete overlap, may not be so when an additional axis is taken into account. Since we can never be sure that we have measured all relevant axes in describing the niches of two species, we can never be sure that the two niches are the same. Hence, we cannot disprove the principle.

9.6 Resource partitioning and habitat selection

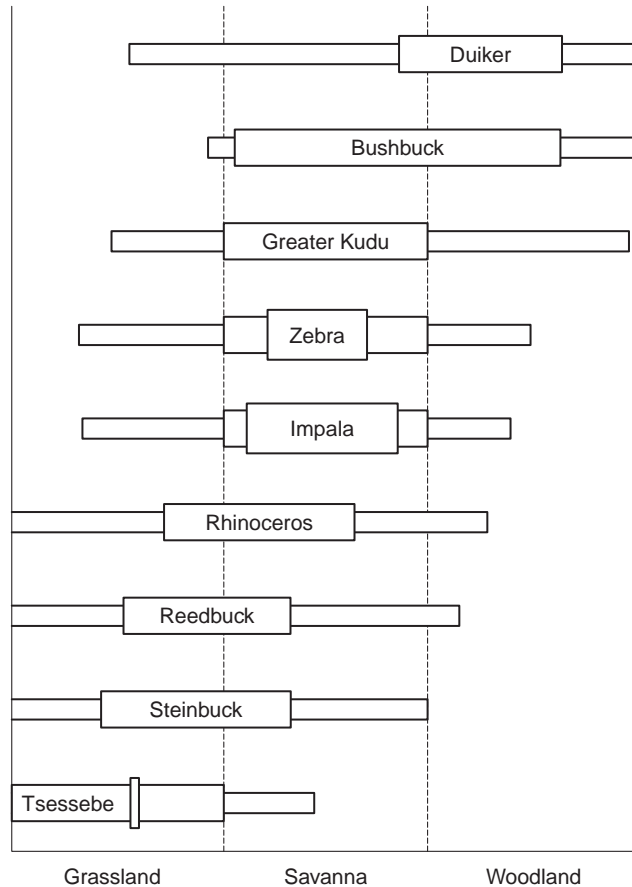
9.6.1 Habitat partitioning

Despite these problems with the competitive exclusion principle, it underlies the numerous studies of habitat partitioning amongst groups of coexisting species. Lamprey (1963) described the partitioning of habitats by species of savanna antelopes in eastern Africa. A similar study by Ferrar and Walker (1974) showed how various antelopes in Zimbabwe used the three habitat types of grassland, savanna, and woodland (Fig. 9.10). In both cases there was partitioning as well as overlap.

Similar studies by Wydeven and Dahlgren (1985) show partitioning of both habitat and food in North American ungulates (Fig. 9.11). In Wind Cave National Park elk and mule deer have similar winter habitat choices, as do pronghorn and bison, but these pairs have very different diets. For example, the diet of bison contains 96% grass as against 4% for pronghorn.

Interspecific overlap in the diet niches of two sibling bat species (*Myotis myotis*, *M. blythii*) of Switzerland shows niche partitioning: *M. myotis* feeds largely on ground insects (carabid beetles) whereas *M. blythii* feeds mostly on grass-dwelling insects (bush crickets). This allows coexistence within the same habitats (Arlettaz *et al.* 1997). MacArthur (1958), in a now classic paper, described the different feeding positions

Fig. 9.10 Habitat partitioning and overlap by ungulates in Kyle National Park, Zimbabwe. The width of the boxes reflects the degree of preference. (After Ferrar and Walker 1974.)



of five species of warblers within conifer trees in the northeastern USA. They varied in both height in the tree and use of inner or outer branches. Nudds *et al.* (1994) found habitat partitioning in dabbling ducks in both Europe and North America. Species with a high density of filtering lamellae in their bills (fine filter feeders) tended to live in deep water with short, sparse vegetation compared with those species with few lamellae which lived in shallow water with tall, dense vegetation.

9.6.2 Limiting similarity

As we have mentioned above it should not be surprising that species divide up the resource available to them. However, Gause's principle implies that there should be a limit to the similarity of niches allowing coexistence of two species. Earlier studies predicted values of limiting similarity based on theoretical arguments (MacArthur and Levins 1967). If the distance between the midpoints of species distributions along the resource axis is d and the standard deviation of the curves (such as those in Fig. 9.7a) is w (the relative width) then limiting similarity can be predicted from the ratio d/w . However, various assumptions, such as the curves must be similar, normally distributed, and along only one resource axis, make this approach unrealistic.

Pianka *et al.* (1979) asked: how much would niches overlap if resources were allocated randomly among species in a community? A frequency distribution of niche overlaps generated from randomly constructed communities is shown in Fig. 9.12.

Fig. 9.11 (a) Diet and (b) winter habitat use of elk, mule deer, pronghorn, and bison in Wind Cave National Park, South Dakota. Where habitat choice is similar there are major differences in diet. (Data from Wydeven and Dahlgren 1985.)

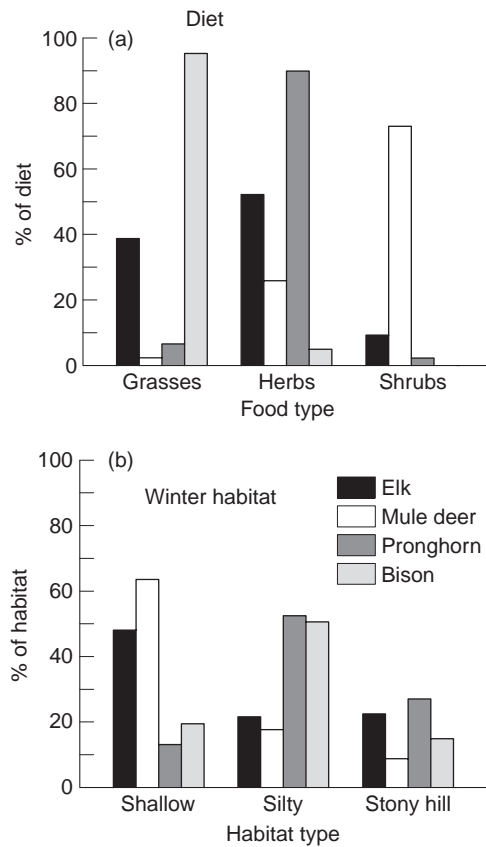
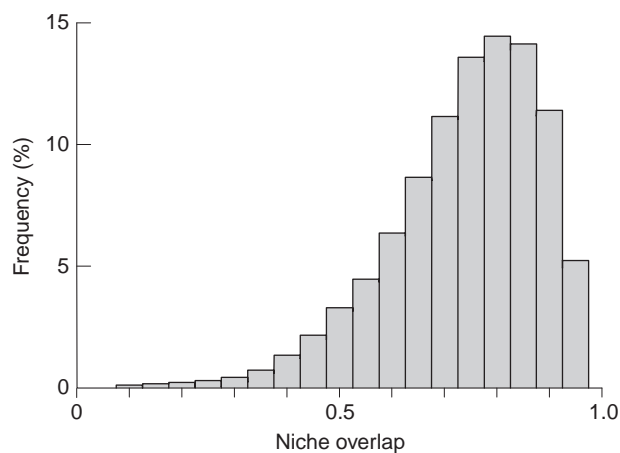
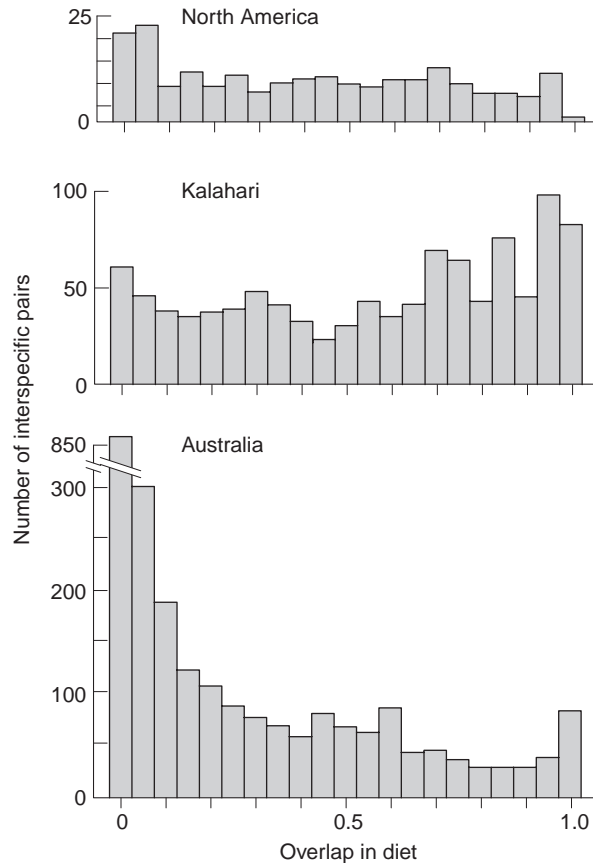


Fig. 9.12 Frequency distribution of niche overlaps in 100 randomly constructed communities with 15 species and five equally abundant resource states. (After Pianka *et al.* 1979.)



This can be compared with distributions of observed overlap in diets of desert lizards from 28 sites on three continents (Fig. 9.13). Those in the Kalahari desert of southern Africa showed the greatest degree of overlap (because one food type, termites, comprised a large amount of the diet), and those in Australia the least. In no case were observed distributions similar to the random distributions: there were far more

Fig. 9.13 Distributions of observed overlap in the diets of desert lizards. Dietary overlap is higher in Kalahari lizards, where termites comprised 41% of the diet. (After Pianka *et al.* 1979.)



species pairs with small overlaps than would be predicted by chance, implying that interspecific competition was causing niche segregation.

9.6.3 Habitat selection from field data

As we have seen, species usually differ from each other by choosing different resources such as food types, habitats, etc. We call this choice **habitat selection**. One approach to measuring the competition coefficients has been to look at the variation of species density in different habitats. First, the variation in density due to habitats, and other resources, is estimated by statistical procedures such as multiple regression (Crowell and Pimm 1976). Then the remaining variance should be attributable to interspecific competition with another identifiable species. An example of this approach is given by Hallett (1982) in a study of 10 desert rodent species in New Mexico. He measured habitat variables related to the common plants such as number of individuals, plant height, distance to nearest plant from trap, and percent cover. Regression analysis was used to partition the variance in capture frequency at trap stations due to habitat variables and competitors. Competition was observed within one group of three species, *Perognathus intermedius*, *Perognathus penicillatus*, and *Peromyscus eremicus* (Table 9.3). Although the competitive effects differed from year to year, they were not random. Also the inhibitory effects were not symmetrical: thus *P. eremicus* always had a greater effect on the other two species than the reverse, and similarly *P. intermedius* had a greater effect on *P. penicillatus* than vice versa.

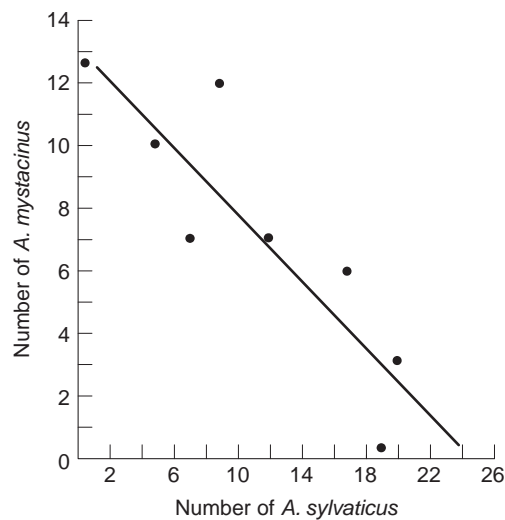
Table 9.3 Matrix of competition coefficients for the *Perognathus*–*Peromyscus* guild for each year. Entries are the partial regression coefficient after removal of the effects of the habitat variables. The coefficients are the effects of the column species (independent variable) on the row species (dependent variable).

	1971		1972			1973		
	PP	PI	PP	PI	PE	PP	PI	PE
PP	...	−0.43*	...	−0.17	−0.42*	...	−0.12	−0.82*
PI	−0.17	...	−0.09	...	0.05	−0.05	...	−0.39*
PE	NI	NI	−0.09	0.19	...	−0.12*	−0.10	...

* $P < 0.05$.

PP, *Perognathus penicillatus*; PI, *Perognathus intermedius*; PE, *Peromyscus eremicus*.
NI, not included in the analysis.

Fig. 9.14 The negative correlation in numbers of two woodmice species (*Apodemus mystacinus* and *A. sylvaticus*) in Israel. (After Abramsky 1981.)



Abramsky (1981) used a similar regression method to look at interspecific competition and habitat selection in two sympatric rodents, *Apodemus mystacinus* and *A. sylvaticus*, in Israel. Plotting the densities of the two species in different habitats against each other (Fig. 9.14) indicated a negative relationship and suggested that there may be interspecific competition operating. However, he found that species abundances could have been the result of habitat differences alone; the effect of the presence of the other species was negligible in this case, implying no competition.

There are problems with the regression method, some of which are outlined by Abramsky *et al.* (1986). One is that if sympatric populations of different species differ greatly in average abundance, then estimates of their variance and regression coefficients are distorted. In turn estimates of competition are unreliable. A second problem lies in the assumption of constant competition coefficients; if competition is weak when populations are close to equilibrium (which we assume is when regressions from field populations are estimated), but strong when disturbed from equilibrium (the situation in perturbation experiments), then regression analysis is likely to miss competitive effects while experiments will indicate their presence. A third problem is that we can never be sure that we have accounted for all the variability

in density at various sites from environmental factors; there may be some factor that has been overlooked to account for the remaining variability instead of attributing it to interspecific competition.

9.6.4 *The theory of habitat selection*

Since species prefer to use some habitats over others, we ask how does this choice change when resources become limiting? There are two hypotheses that we should consider. We start with the **theory of optimal foraging** which predicts that when resources are not limiting, species should concentrate their feeding on the best types of food or the best types of habitats and ignore the others no matter how abundant they are. When resources are limiting, a species should expand its niche to include other types of food, habitat, etc. This is the expected response under intraspecific competition.

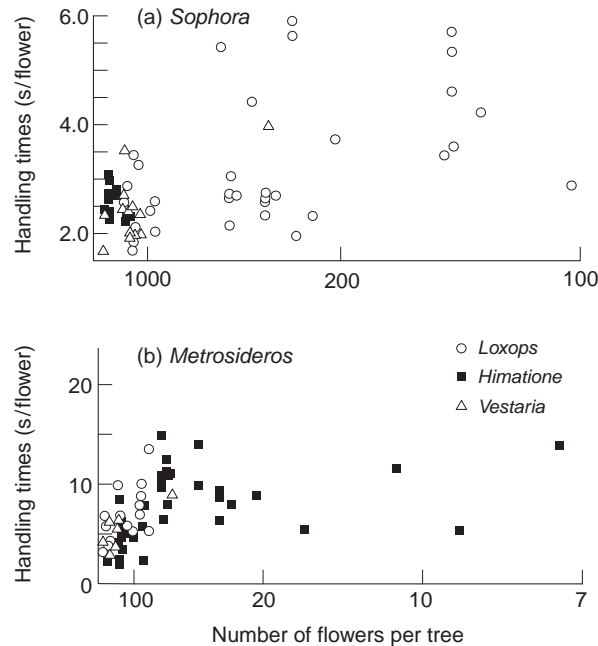
When two species are present one might expect both to respond to declining resources by expanding their niches and so increase the overlap. However, Rosenzweig's (1981) **theory of habitat selection** introduces a second hypothesis. This predicts that when resources are limiting, species should contract their niches as a result of interspecific competition. He considered two different situations: we start by assuming that there are two species, 1 and 2, and two habitats, A and B. In the first case, called the **distinct preference** case, both species use both habitats but each prefers to use a different one (i.e. species 1 treats A as the better and B as the poorer habitat, while species 2 does the reverse). In the second case, the **shared preference** case, again both species use both habitats, but now both treat the same habitat A as the better and B as the poorer one.

In either case we should first consider the habitat choice of a species when no competitors are present. Under conditions of abundant resources, such as food, a species should confine itself to its preferred habitat. As density increases and resources become limiting through the feeding of other individuals, the species will continue to remain in the better habitat (A) so long as the food intake rate is greater than what it would be in the poorer habitat (B). At some point, density in habitat A increases so that intake rate falls until it equals that in habitat B: at this stage the species should not confine itself to A but should expand its habitat use in such a way that densities keep intake rates similar in the two habitats. The intake rate at which the species changes from one to two habitats is called the **marginal value**.

Now we consider what happens when there is a competitor present and resources are limiting. The outcome depends on which of the two preference cases occurs. First, in the distinct preference case each species will confine itself to its preferred habitat rather than expand into the other habitat. Therefore, when resources are limiting, species will specialize, contract their niches and reduce overlap. When resources are abundant they should use either one or both habitats depending on their intake rates in the two habitats. Second, in the shared preference case we have to assume that one of the species (1) is dominant and can exclude by behavior, or other means such as scent marking, the second species from the preferred habitat A. If species 2, the subordinate, is to coexist with species 1 then it must be more efficient at using the less preferred habitat B than species 1. If the dominant is more efficient in both habitats then it will exclude species 2. Therefore, when resources are limiting, one species – the dominant – will not change its habitat choice. In contrast, the subordinate will change its choice from A to B: the competitive effect is asymmetrical, with the dominant having a large effect on the subordinate while the reverse effect is small.

Fig. 9.15

Demonstration of distinct and shared preferences in habitat selection by three species of honeycreepers in Hawaii. The two main flowering trees are (a) *Sophora* and (b) *Metrosideros*. At low flower numbers *Loxops* (○) fed on *Sophora*, and *Himatione* (■) fed on *Metrosideros*, showing “distinct preference.” *Vestaria* (△) fed on both trees, excluding the other species, but only at high flower numbers, indicating “shared preference.” Note the reverse scale on the x-axis. (After Pimm and Pimm 1982.)



In a test of these hypotheses Pimm and Pimm (1982) recorded the feeding choices of three nectar-feeding bird species (*Himatione*, *Loxops*, *Vestaria*) on the island of Hawaii. There were two main tree species, *Metrosideros* and *Sophora*, which came into flower at different times of the year. The evidence for the distinct preference case is seen in Fig. 9.15. When the number of flowers is high, all three species feed on both trees. When flowers per tree are low (and assuming that this indicated limiting resource) only *Loxops* feed on *Sophora*, and only *Himatione* feed on *Metrosideros*. Thus, both species reduce their niche width and specialize. There was also evidence of shared preference. *Vestaria* feed on both tree species but only at high flower numbers, and physically exclude the other species by visual and vocal displays. In contrast, both *Himatione* and *Loxops* spend much of their feeding time on trees with few flowers. Thus, these two species are confined to poorer feeding areas during times when resources are low, as predicted by the theory.

Rosenzweig's theory predicts that niches contract when resources are limiting and there is interspecific competition. We have seen that the Hawaiian honeycreepers may conform to the predictions, but what about other species? Information from wildlife both agrees and disagrees with the predictions. The overlap in diet of sympatric mountain goats (*Oreamnos americanus*) and bighorn sheep (*Ovis canadensis*) is high in summer but reduced in winter (Dailey *et al.* 1984), as predicted by the theory. In ducks we have already seen that during winter there is a decrease in overlap (Fig. 9.9). Burning grasslands increases the nutrient content of regenerating plants and may produce locally abundant food. Under these conditions mountain goats and mule deer (*Odocoileus hemionus*) actually increase dietary overlap (Spowart and Thompson Hobbs 1985). In contrast, elk and deer in natural forests increased dietary overlap in winter when resources were assumed to be least available, contrary to expectation (Leslie *et al.* 1984).

We should note that we do not have actual measures of the food supply in these examples, so we cannot be sure that we are seeing competition. In Serengeti, Tanzania, wildebeest are regulated by lack of food in the dry season (Mduma *et al.* 1999), so that overlap with this species at this time should result in competition. However, overlap in both diet and habitat between wildebeest and several other ungulate species increases or does not change between wet and dry seasons (Hansen *et al.* 1985; Sinclair 1985). One interpretation could be that interspecific competition is asymmetrical, with the impact of the rarer ungulates on the numerous wildebeest being real but very slight, while the reverse does not occur because these other ungulates are kept at low density by predation (Sinclair *et al.* 2003).

9.7 Competition in variable environments

So far we have discussed the patterns of occupancy and utilization of habitats as if they were constants for a species, or that they changed only seasonally. However, longer-term studies are now showing that species densities vary in the same habitat and they also change over a longer time scale measured in years. Thus populations may go through periods when there are abundant resources and, although there is overlap with other species, even at the supposedly difficult time of year there is no competition (Fig. 9.16). Occasionally there are periods of resource restriction and it is only at these times that one sees competition and niche separation (Wiens 1977).

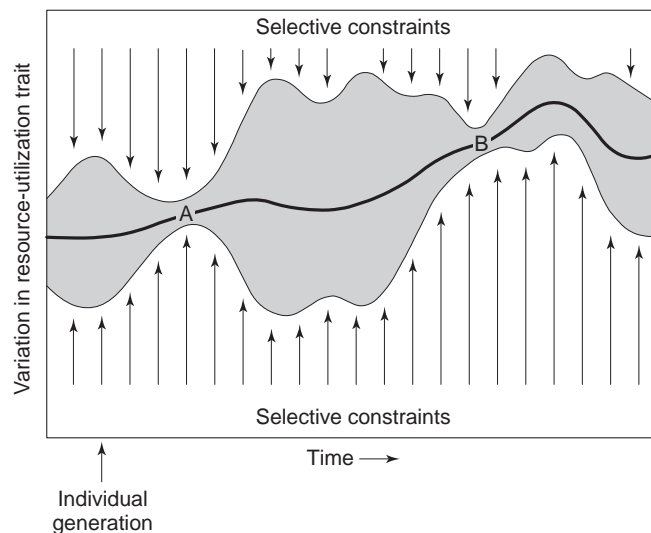
9.8 Apparent competition

9.8.1 Shared predators

Some of the predicted outcomes from interspecific competition include the reduction of populations, the contraction of niches, and exclusion of species from communities. However, these predictions are also to be expected when species have non-overlapping resource requirements but share predators, especially when predators can increase their numbers fast.

Let us suppose there is a predator that is food limited, and which feeds on two prey species. The prey are both limited by predation and not by their own food supplies. If species 1 increases in number then this should lead to more predators, which in turn will depress species 2 numbers. This result is called **apparent competition**

Fig. 9.16 Changes over time in the mean (thick line) and variance (shaded area) of a selective constraint such as resource availability. At times A and B there are “bottlenecks” when competition is more likely. (After Wiens 1977.)



because it produces the same changes in prey populations as would be predicted from interspecific competition (Holt 1977, 1984). Examples of apparent competition are given in Section 9.10.2 and Chapter 21, where predators are causing the demise of secondary prey, the rare roan antelope in Kruger National Park, South Africa (Harrington *et al.* 1999; McLoughlin and Owen-Smith 2003), and the wildebeest in Manyara National Park, Tanzania, as a result of a high abundance of buffalo, the primary prey.

If two prey species live in the same habitat, as in the wildebeest and buffalo example in Manyara, then at high intensities of predation coexistence is unlikely. On the other hand, coexistence is promoted if the two species select different habitats, that is, niche partitioning occurs.

Another version of apparent competition can occur through shared parasites. One species can be a superior competitor if it supports a parasite which it transmits to a more vulnerable species. For example, when gray squirrels (*Sciurus carolinensis*) were introduced to Britain, they brought a parapox virus that reduced the competitive ability of the indigenous red squirrel (*S. vulgaris*) (Hudson and Greenman 1998). The latter has largely been displaced, occurring now in only a few small locations of its former range. Gray squirrels are displacing red squirrels through competition in Italy, and could be spreading through Europe (Wauters and Gurnell 1999).

9.8.2 Implications

Since the observed responses of prey populations to changes in predator numbers are similar to those from interspecific competition, we cannot infer such competition simply from observations or even experiments that show either changes in species population size or niche shifts. We need to know (i) whether resources are limiting; and (ii) the predation rates and predator numbers.

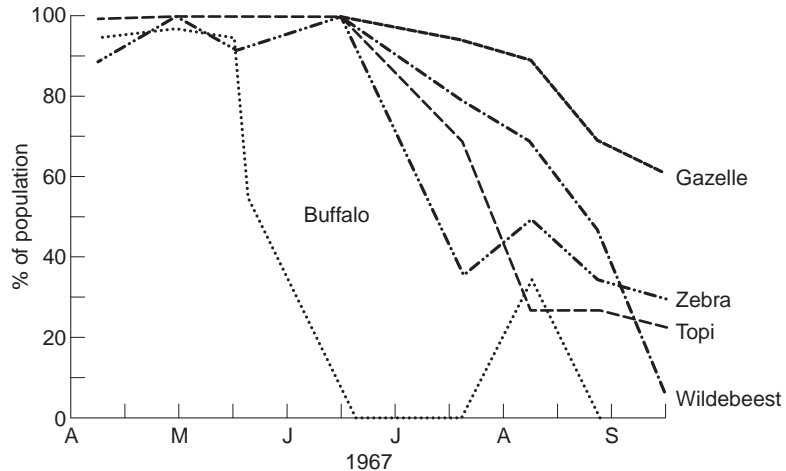
9.9 Facilitation

9.9.1 Examples of facilitation

Facilitation is the process whereby one species benefits from the activities of another. In some cases the relationship is **obligatory** as in the classic example of the nereid worm (*Nereis fucata*), which lives only in the shell of hermit crabs (*Eupagurus bernhardus*). The crabs are messy feeders and scraps of food float away from the carcass that is being fed upon; these scraps are filtered out of the water by the worm. While the worm benefits, the crab appears not to suffer any disadvantage (Brightwell 1951). In other cases the relationship may be **facultative**, by which we mean that the dependent species does not have to associate with the other in order to survive, but does so if the opportunity arises. Thus, cattle egrets (*Ardea ibis*) often follow grazing cattle in order to catch insects disturbed by these large herbivores. Although the birds increase their prey capture rate by feeding with cattle, as they probably do by following water buffalo (*Bubalus bubalus*) in Asia and elephants and other large ungulates in Africa, they are quite capable of surviving without large mammals (McKilligan 1984). The European starling (*Sturnus vulgaris*) also follows cattle on occasions. In contrast, its relative in Africa, the wattled starling (*Creatophora cinerea*), seems always to follow large mammals and in Serengeti they migrate with the wildebeest like camp followers.

Vesey-Fitzgerald (1960) suggested that there was grazing facilitation amongst African large mammals. Lake Rukwa in Tanzania is shallow and has extensive reedbeds around the edges. The grasses, sedges, and rushes can grow to several meters in height, and in this state only elephants can feed upon the vegetation. As the elephants feed and trample the tall grass they create openings where there is lush

Fig. 9.17 The proportion of the population of different ungulate species using short grass areas on ridge tops (upper catena) in Serengeti. The larger species leave before the smaller at the start of the dry season. (After Bell 1970.)



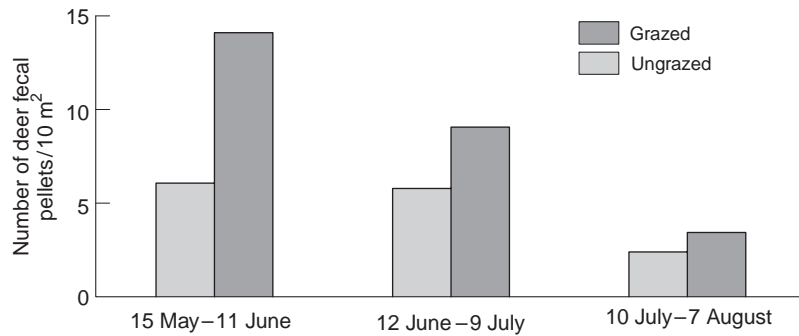
regenerating vegetation. This provides a habitat for African buffalo, which in turn provide short grass patches that can be used by the smaller antelopes such as topi. In this case elephants are creating a habitat for buffalo and topi that would not otherwise be able to live there. Therefore, the presence of elephants increases the number of herbivores that can live in the Lake Rukwa ecosystem. Vesey-Fitzgerald called this sequence of habitat change in the grasslands a **grazing succession**.

Bell (1971) has described a similar grazing succession amongst the large mammals of Serengeti. In certain areas of Serengeti there is a series of low ridges bounded by shallow drainage lines. The ridges have sandy, thin soils and support short, palatable grasses. The drainage lines have fine silt or clay soils that retain water longer than those on the ridges and so support dense but coarse grasses, which remain green long into the dry season. Between these two extremes there are intermediate soil types on the slopes. The whole soil sequence from top to bottom is called a **catena**. In the wet season when all areas are green, all five non-migratory species (wildebeest, zebra, buffalo, topi, and Thomson's gazelle) feed on the ridge tops. Once the dry season starts the different species move down the soil catena into the longer grass in sequence, with the larger species going first (Fig. 9.17). Thus, zebra is one of the first species to move because it can eat the tough tall grass stems. By removing the stems, the zebra make the basal leaves in these tussock grasses more available to wildebeest and topi, and these in turn prepare the grass sward for the small Thomson's gazelle. Thus, there is a grazing succession.

Zebra, wildebeest, and Thomson's gazelle also have much larger migratory populations in Serengeti separate from the smaller resident populations discussed above. It is tempting to think that the movements of these migrants follow the same pattern as those of the resident populations. Indeed, McNaughton (1976) has shown that migrating Thomson's gazelle prefer to feed in areas already grazed by wildebeest because these areas produce young green regrowth not found in ungrazed areas. The gazelle take advantage of this growth, which was stimulated by the grazing, and so benefit from the wildebeest.

The relationship between the migrating zebra and wildebeest is more complex. Although zebra usually move first from the short grass plains to the long grass dry-season areas, the wildebeest population (1.3 million), which is much larger than

Fig. 9.18 Facilitation of deer grazing by cattle is demonstrated by deer fecal-pellet groups on cattle-grazed plots during each of the 3 months of study. Deer preferred to graze plots used by cattle the previous winter. (After Gordon 1988.)



that of zebra (200,000), often do not follow the zebra but take their own route and eat the long dry grass. Therefore, most migrant wildebeest obtain no benefit from the zebra. In contrast, zebra may be benefiting from the wildebeest for a completely different reason. In the wet season, when there is abundant food, many zebra graze very close to the wildebeest, and by doing so they can avoid predation because most predators (lions and spotted hyenas (*Crocuta crocuta*)) prefer to eat wildebeest. Only if there are no wildebeest within range will predators turn their attention to zebra. Therefore, it pays zebra to make sure there are wildebeest nearby. In the dry season, however, zebra compete with wildebeest for food. Zebra, therefore, show habitat partitioning and avoid the wildebeest. However, by doing so they probably make themselves more vulnerable to predators again (Sinclair 1985). Thus, zebra have to balance the disadvantages of predation if they avoid wildebeest with competition if they stay with the wildebeest. We can see a seasonal change from facilitation in the wet season when there is abundant food, to competition in the dry season when food is regulating the wildebeest.

An example of facilitation has been recorded on the island of Rhum, Scotland. There cattle were removed in 1957 and reintroduced to a part of the island in 1970 where they grazed areas used by red deer. Pasture used by cattle in winter results in a greater biomass of green grass in spring compared with ungrazed areas. Gordon (1988) found that deer preferentially grazed areas in spring that had previously been used by cattle (Fig. 9.18), and subsequently there were more calves per female deer.

On the North American prairies both black-tailed prairie dogs (*Cynomys ludovicianus*) and jackrabbits (*Lepus californicus*) benefit from grazing by cattle. If grazing is prevented, then the long grass causes prairie dogs to abandon their burrows. At a site in South Dakota where cattle were fenced out, there were half as many burrows as on adjacent areas where grazing was continued. Snell and Hlavachick (1980) showed that a large prairie dog site of 44 ha could be reduced to a mere 5 ha by the elimination of cattle grazing in summer to allow the grass to grow. Presumably under natural conditions when American bison grazed the prairies there was facilitation by bison allowing prairie dogs to live in the long grass prairies. Facilitation could be mutual because both pronghorn and bison respond to the vegetation changes caused by prairie dogs, both species using prairie dog sites (Coppock *et al.* 1983; Wydeven and Dahlgren 1985; Huntly and Inouye 1988; Miller *et al.* 1994).

This example illustrates two management points which follow from the understanding of the interaction (facilitation) between large mammal grazers and prairie dogs:

(i) a simple management program (through grazing manipulation) could be devised to control the prairie dogs, without the use of harmful poisons which could affect other species; and (ii) in many areas prairie dogs are becoming very scarce and their colonies need to be protected. In addition, the black-footed ferret (*Mustela nigripes*), one of the rarest mammals in the world, depends entirely on prairie dogs and it is thought that their very low population has resulted from the decline in prairie dog populations. The conservation of both species would benefit from the manipulation of grazing practices.

In another example where facilitation improved management for wildlife, Anderson and Scherzinger (1975) showed that ungrazed grassland resulted in tall, low-quality food in winter for elk. Cattle grazing in spring maintained the grass in a growing state for longer. If cattle were removed before the end of the growing season, the grasses could regrow sufficiently to produce a shorter, high-quality stand for elk; their population increased from 320 to 1190 after grazing management was introduced.

In Australia, rabbits prefer very short grass. Rangelands that have been overgrazed by sheep benefit rabbits, through facilitation, and rabbit numbers increase. When sheep are removed and long grass returns, rabbit numbers decline. In Inner Mongolia, China, the substantial increase in livestock numbers since 1950 has produced a grass height and growth rate that favors Brandt's vole (*Microtus brandti*) populations so that there has been an increase in the frequency of population outbreaks of this species (Zhang *et al.* 2003).

The saltmarsh pastures of Hudson Bay in northern Canada are grazed by lesser snow geese (*Chen caerulescens*) during their summer breeding (Bazely and Jefferies 1989; Hik and Jefferies 1990; Wilson and Jefferies 1996). The marshes are dominated by the stoloniferous grass *Puccinellia phryganodes* and the rhizomatous sedge *Carex subspathacea*. At La Perouse Bay some 7000 adults and 15,000 juvenile geese graze the marsh, taking 95% of *Puccinellia* leaves. These are nutritious, with high amounts of soluble amino acids. From exclosure plots it was found that natural grazing by geese increased productivity by a factor of 1.3–2.0. Experimental plots with different levels of grazing by captive goslings showed that above-ground productivity of *Puccinellia* was 30–100% greater than that of ungrazed marsh. In addition, the biomass (standing crop) of the grass was higher if allowed to regrow for more than 35 days following clipping. Immediately after the experimental grazing the biomass was less than the ungrazed plots, so that at some point between then and the eventual measurements the biomass on the treated and untreated plots was the same. Even so, the production rate of shoots was higher on the grazed sites. Other experimental plots where grazing was allowed but from which goose feces were removed showed that biomass returned to the level of control plots, but no further. Thus, it appears that goose droppings, which are nitrogen rich and easily decomposed by bacteria, stimulate growth of *Puccinellia*. Geese, therefore, benefit each other from their grazing by fertilizing the grass, a form of intraspecific facilitation.

In summary, facilitation occurs when one species alters a habitat, or creates a new habitat, which allows the same or other species to benefit. We have discussed grazing systems, in particular, but the concept applies in many other cases. For example, many hole-nesting birds and mammals in North America such as wood ducks (*Aix sponsa*) and flying squirrels (*Glaucomys sabrinus*) depend on woodpeckers to excavate the holes, a form of facilitation. Knowledge of such interactions is important for the proper management and conservation of ecosystems.

9.9.2 Do grasses benefit from grazing?

If a species such as Thomson's gazelle benefits from the grazing effects of wildebeest due to the increased productivity of the plants, then do the plants themselves benefit? In other words, what benefits do the plants receive from being grazed and growing more? In evolutionary terms (see Chapter 3) we have to rephrase this as, "Does herbivory increase the fitness of individual plants?" In ecological terms one may ask, "Does the plant grow more after herbivory?"

The studies of lesser snow geese on the saltmarshes of Hudson Bay, which we have discussed above, are now showing that the grass *Puccinellia* comes in different genotypes (Jefferies and Gottlieb 1983). Nineteen grazing experiments have shown that under grazing there is selection for those genotypes that are fast growing. These types have the ability to take up the extra nitrogen from the goose feces and seem to outcompete slower-growing genotypes. This is, therefore, an evolutionary benefit from grazing. Plots where grazing is prevented show that, after 5 years, change to slower-growing genotypes was only just beginning. The more immediate ecological benefit from grazing again comes from the addition of nutrients resulting in a 30–50% increase in biomass.

In general there are few studies that show plants increasing their fitness as a result of herbivory (Belsky 1987). In contrast, we can look at communities of plants and see that if the majority of plants, such as grasses, can tolerate grazing (i.e. survive despite herbivory) a few other intolerant species in that community may not survive due to inadvertent feeding or trampling by large mammals (i.e. apparent competition rather than true competition between plants). This may be simply a consequence of grazing and not necessarily an evolutionary advantage for the grass species. Nevertheless, McNaughton (1986) has argued in opposition to Belsky that grasses and grasslands have evolved in conjunction with their large mammal herbivores, especially in Africa. From an evolutionary point of view a grass individual that by chance evolved an antiherbivore strategy (such as the production of distasteful chemicals) should be able to spread through the grassland. We have to surmise at this stage that antiherbivore adaptations are constrained in some way; for example, it could be that production of distasteful chemicals results in the plant being less successful, in root competition, or in the uptake of nutrients, as in the example of lesser snow geese grazing.

On the surface it appears disadvantageous for a grass to grow more as a response to grazing because it would provide more food and invite further grazing. However, growth could also be viewed as a damage repair mechanism that is making the best of a bad situation (i.e. the grass may lose fitness less by growing than by not doing so).

In summary, we know too little about both the ecological and evolutionary consequences of herbivory on plants. We are left with many questions and opposing views, and more work is needed.

9.9.3 Complex interactions

Competition, parasitism, and predation are all processes that have negative effects on a species. However, when they act together they may end up having a beneficial effect. For example, acorns of English oak (*Quercus robur*) are parasitized by weevils and gall wasps, and are eaten by small mammals. Very high mortality rates are imposed on healthy acorns by small mammals, but parasitized acorns are left alone. While most of the parasitized acorns also die, some survive and are avoided by the small mammals. Thus, higher survivorship and hence fitness occurs when the plant is parasitized (Crawley 1987; Semel and Andersen 1988).

9.10 Applied aspects of competition

9.10.1 Applications

It is important that we should understand the underlying concepts of interspecific competition if we are to comprehend how species might or do actually interact in the field. There are several applications where we need to be aware of potential competition: (i) in conservation where we might have to protect an endangered species from competition with another dominant species; (ii) in managed systems such as rangelands and forests where there could be competition between domestic species and wildlife – for example an increase in livestock or the expansion of rangeland might cause the extinction of wildlife species, or wildlife might eat food set aside for the domestic animals; and (iii) if we want to introduce a new species to a system, for example a new game bird for hunting, and there could be competition from other resident species.

9.10.2 Conservation

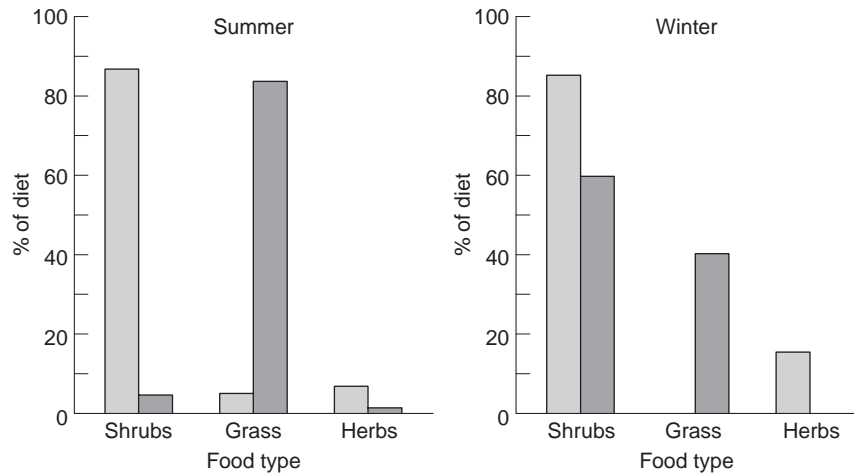
Let us imagine a situation where we want to conserve a rare species but we are concerned about possible competition from a common species. For example, roan antelope (*Hippotragus equinus*), a fairly rare species, were released in Kruger National Park, South Africa, as part of a conservation program. There were concerns that the numerous wildebeest would exclude the roan antelope. In this case the management response was to cull the wildebeest (Smuts 1978). More recent evidence indicates that predators, supported by an abundant zebra population, are limiting and even excluding this rare species (Harrington *et al.* 1999; McLoughlin and Owen-Smith 2003). Thus, apparent competition is the dominant process here. A similar example involved the extremely rare Arabian oryx (*Oryx leucoryx*). A few of the last remaining individuals of this species were captured in Arabia in the early 1960s and taken to the San Diego zoo. Their numbers increased and some have been successfully reintroduced to Oman (Stanley Price 1989).

In both of these examples it would be important to detect whether there was competition with resident species. We have seen that simple measures of overlap or even changes of overlap with season may not be good indicators of competition. Similarly, observations that an increase in a common species is correlated with a decrease in the rare species does not mean that competition is the cause because of the problem of apparent competition. These measures are necessary but not sufficient. In addition we would need a measure of: (i) resource requirement; (ii) availability of limiting resources and demonstration that one is in short supply; and (iii) the predation rates on both the target species and alternative prey.

A second kind of problem comes from changes in habitat. Assume there is coexistence and habitat partitioning between two species along the lines of Rosenzweig's shared preference hypothesis described above. Since studies of diet and habitat selection would show that both species prefer the same habitat, one may be tempted to manage an area by increasing the preferred habitat at the expense of the other habitats. In this case, however, only one species, the dominant, would benefit and the other would decline. The breeding habitats of the yellow-headed and red-winged blackbirds (Orlans and Willson 1964) may be a case in point. Both species prefer deeper-water marshes but one may predict that increasing the depth of a marsh where both occur, thereby leaving little shallow water, may well result in the exclusion of the red-winged blackbird.

In Lake Manyara National Park, Tanzania, there is a habitat consisting of open grassland on the lake shore which is used by wildebeest. Adjacent to this shoreline is savanna consisting of longer grass with scattered trees and shrubs preferred by African

Fig. 9.19 The percentage of the diet of white-tailed deer (open bars) and cattle (shaded bars) made up of shrubs, grasses, and herbs. Diet overlap increased in winter when food was limiting. (Data from Thill 1984.)



buffalo. In 1961 heavy rains caused the lake levels to rise and flood the open grasslands, a situation which remained for the rest of the 1960s. The wildebeest were forced to use the savanna habitat, which they did not prefer, and after 4 years the population went extinct. On the surface this appeared to be due to competition with buffalo. Closer inspection of the situation showed that lions, whose densities were high because of the high buffalo population, had eradicated the wildebeest. Wildebeest normally escape predation by running, which they can do in habitats with short grass and little cover for ambush by predators. Once wildebeest were confined to the savanna they were less capable of avoiding lions. Buffalo, on the other hand, avoid predators by hiding in thickets and defending themselves with their horns, and this they could do in savanna but not on the open grassland. Thus, each prey species had its own specialized antipredator habitat that allowed coexistence between the prey species, as predicted by Holt's (1977) "apparent competition" hypothesis. Once this habitat partitioning broke down, the predator was able to eliminate one of the species. The process of apparent competition explains these observations better than true competition.

9.10.3 Competition between domestic species and wildlife

There are a number of studies designed to detect whether there is competition between livestock and wildlife. Thill (1984) recorded the seasonal diets of cattle and white-tailed deer in three forested and two clear-cut sites in Louisiana pine forests. Woody plants made up more than 85% of the diet of deer on the forest sites throughout the year (Fig. 9.19). For cattle diets these plants made up less than 16% in summer and fall but rose to 60% in winter and to 48% in spring. The overlap between the two species in overall diet was highest in winter at 46% and lowest in summer at 12%. In contrast, on cleared sites deer continued to eat mainly woody plants but cattle ate more than 80% grass year round. Diet overlap was only 17% in summer and fell to 10% in winter. Since the two species were in the same habitat and there did not appear to be predators, there could be a real possibility for interspecific competition if cattle were confined to forest sites; in fact most of them stayed on the open sites. It is possible that because cattle and deer have not evolved together we do not see the expected decrease in overlap in winter, so that competition is increased rather than avoided at this time.

Thill (1984) points out the advantages for multiple use management derived from the diet partitioning. As forest practices intensify, forest ages decrease and the young stands become impenetrable without artificial clearing. They are also poor areas for deer forage. If cattle were used to graze these sites they could be kept open and so benefit deer by improving accessibility and increasing production of the second growth deer food plants. This presumes that increasing deer numbers is the management objective. We should recognize that deer can have negative impacts, particularly on rare plants and birds (McShea *et al.* 1997), so management of deer needs to be carefully evaluated.

Hobbs *et al.* (1996) manipulated elk densities in randomized block experiments in sagebrush grassland to study the effects of competition with cattle. The effects of elk on cattle exhibited a threshold where low densities of elk had no effect but above a certain density there were both competition and facilitation effects. Food intake declined in direct proportion to elk density because elk reduced the biomass of standing dead grass in winter. There were some weak facilitatory effects of elk grazing through an increase in digestibility and nitrogen content of the remaining grass available to cattle.

Cattle can also have indirect competitive effects by altering habitat structure. In a study of bird communities using the riverine shrub willow habitats in Colorado, Knopf *et al.* (1988) found that cattle grazing altered the structure of the shrubs but not the plant composition. Areas with only summer grazing contained larger bushes widely spaced and with few lower branches when compared with those areas that experienced only winter grazing. The difference in structure affected migratory bird species according to how specific their habitat preferences were. Densities of those with wide habitat preference (e.g. yellow warbler (*Dendroica petechia*), song sparrow (*Melospiza melodia*)), did not change between the sites. Those with moderate niche width (American robin (*Turdus migratorius*), red-winged blackbird (*Agelaius phoeniceus*)), were three times more numerous on the winter-grazed sites; while those with narrow niches (willow flycatcher (*Empidonax traillii*), white-crowned sparrow (*Zonotrichia leucophrys*)), occurred only on the winter-grazed sites.

Hayward *et al.* (1997) found from a 10-year enclosure of cattle in riparian habitats of arid zones in New Mexico that small mammals were 50% more abundant in areas where cattle were excluded. Similarly, kangaroo rats (*Dipodomys merriami*) were more abundant in semi-desert shrubland where cattle grazing was reduced (Heske and Campbell 1991), and reptiles were also more abundant (Bock *et al.* 1990).

9.10.4 Introduction of exotic species

Exotic species, those that do not normally live in a country, are introduced for a variety of reasons, and very often they become competitors with the native wildlife. Rabbits in Australia are perhaps the most conspicuous example of this, for they have been implicated in the decline of native herbivores through either direct competition or apparent competition by supporting exotic predators such as foxes (Short and Smith 1994; Short *et al.* 2000; Robley *et al.* 2001). Dawson and Ellis (1979) measured the dietary overlap between the rare yellow-footed rock-wallaby (*Petrogale xanthopus*), the euro (*Macropus robustus*), which is a kangaroo, and two introduced feral species, the domestic goat and European rabbit. During periods of high rainfall the rock-wallaby's diet was mostly of forbs (42–52%) but the proportion of forbs in the ground cover was only 14%. Under drought conditions they still preferred forbs (there was 13% forbs in the diet when forbs were hardly detectable in the vegetation) but trees

and shrubs formed the largest dietary component (44% browse). At this season major components for the other species were: euros, 83% grass; goats, 65% browse; rabbits, 25% browse. The rock-wallabies overall diet overlap was 75% with goats, 53% with rabbits, and 39% with euros. In good conditions dietary overlap was still substantial but lower than when drought prevailed. At that time the overlap was 47% and 45% with goats and euros, respectively. Thus, potential competition was greatest with goats and rabbits and least with the indigenous euro.

In North America the introduced starlings (*Sturnus vulgaris*) and house sparrows (*Passer domesticus*) have competed with the native bluebird (*Sialia sialis*) for nesting sites, with the result that bluebird numbers have declined considerably (Zeleny 1976).

Not all introductions result in competition. Chukar partridge (*Alectoris chukar*) have been introduced to North America as a game bird. Their habitat includes semi-arid mountainous terrain with a mixture of grasses, forbs, and shrubs. In particular, they like the exotic cheatgrass (*Bromus tectorum*). Chukar introductions succeeded only where cheatgrass occurred. These habitat requirements are unlike those of native game birds such as sage grouse (*Centrocercus urophasianus*), and thus little competition has taken place (Gullion 1965). Robley *et al.* (2001) showed that the endangered burrowing bettong (*Bettongia lesurur*) in Australia was able to cope with drought stress much better than rabbits because they could eat a variety of herbs and shrubs that rabbits could not eat. If anything these bettongs could outcompete rabbits. Thus, the decline of these marsupials was due to apparent competition from foxes (Short *et al.* 2000).

9.11 Summary

Interaction between species can be competitive or beneficial. Competition occurs when two species use a resource that is in short supply, but a perceived shortage in itself should not be used as unsupported evidence of competition. Instead, the relationships must be determined by manipulative experiments reducing the density of one to determine whether this leads to an increase of the other. Care should be taken to eliminate other factors such as predation that may cause the response. Facilitation is the process by which one species benefits from the activities of the other. It often takes the form of one species modifying a less suitable food supply to make it more suitable for another species, and where one species modifies a habitat making it more favorable for another.

These two effects – competition and facilitation – can often be manipulated by management to increase the density of a favored species.